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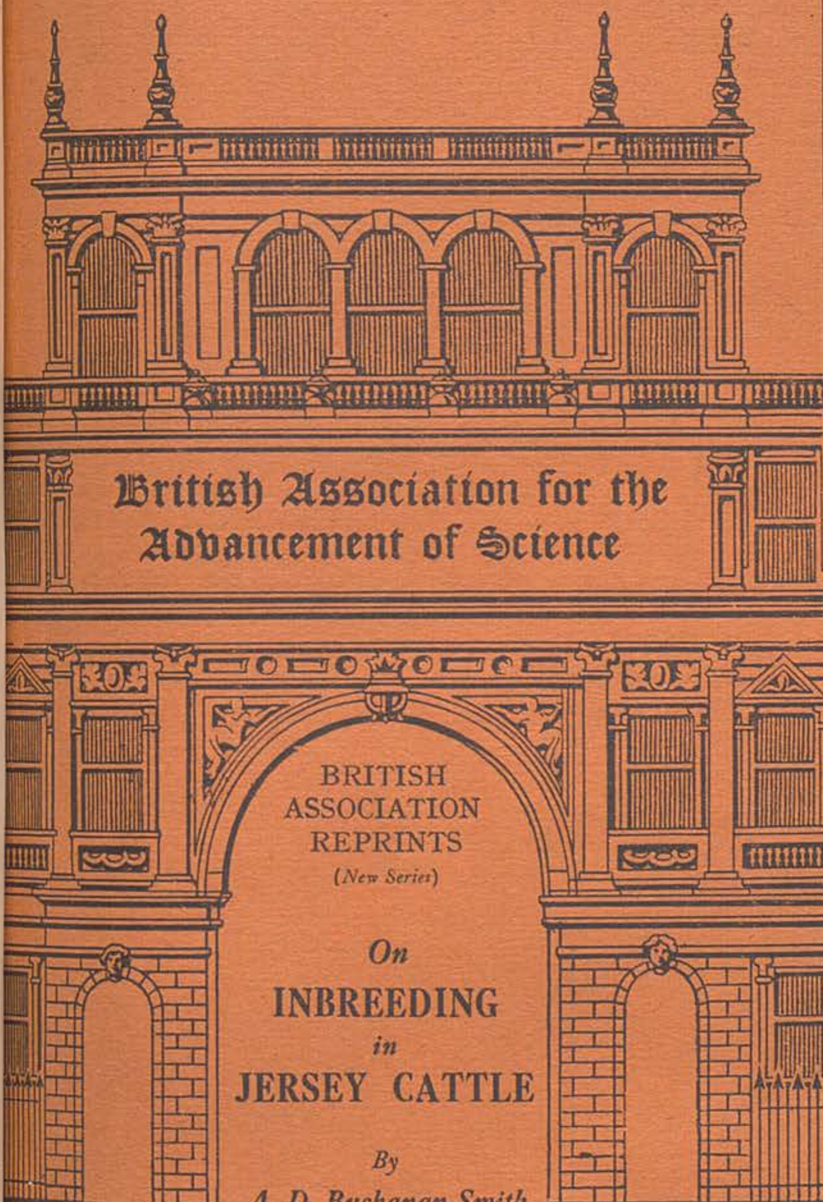

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On INBREEDING *in* JERSEY CATTLE

By
A. D. Buchanan-Smith

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INBREEDING IN JERSEY CATTLE.

THE POSSIBILITY OF YIELD AND QUALITY OF MILK BEING INHERITED IN A SEX LINKED MANNER.

BY

A. D. BUCHANAN SMITH,

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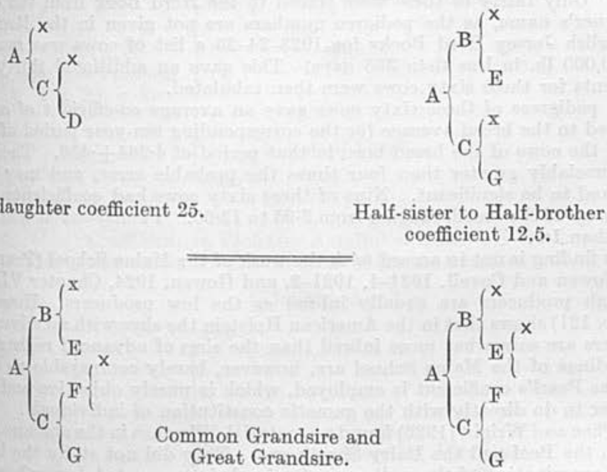
For some time past the methods employed by breeders in the construction of various breeds of commercial livestock have been studied in this department. The analysis of the various breeds has been made by means of Wright's coefficient of inbreeding, which in essence is based on Galton's Law of Ancestral Inheritance, with this important addition, that inbreeding cannot be considered to have full genetic effect on the homozygosity of the animal unless the ancestor to which the animal is inbred appears in the pedigrees of both the sire and dam of that animal. Figure I gives examples of Wright's coefficient. The two lower pedigrees show that, although in both of them the common ancestor, x, is a grandsire and a great grandsire, inbreeding only occurs in the left-hand pedigree since, on the right-hand one, x does not appear as an ancestor of the dam of the individual.

FIGURE I.

Examples of Coefficients of Inbreeding (Wright's).

x = Common Ancestor.



Sire to daughter coefficient 25.

Half-sister to Half-brother coefficient 12.5.

Coefficient 6.25.

Coefficient nil. The common ancestor appears on only the sire's side of the pedigree.

$$\text{Wright's Coefficient } F = (\tfrac{1}{2})^{n+n^1+1}(1+fa)$$

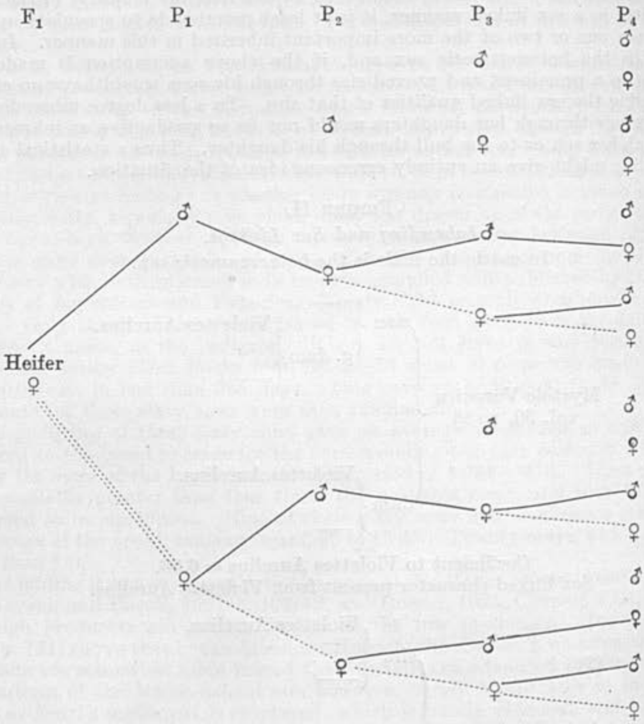
n and n^1 represents the number of generations which the common ancestor is distant from the sire and dam respectively. Fa is the coefficient of inbreeding of the common ancestor.

The writer is indebted to Dr. H. Corner, of Brook House, Southgate, Lond for the direction of his attention to this. Dr. Corner was breeding his herd of Jer along these lines with notable results when unfortunately, owing to an outbrea foot and mouth disease, the herd had to be destroyed. Miss Robertson (19 contributed a paper to the *Journal of Genetics* from statistics of a herd of Kerry ca which had been recorded daily since 1904. The figures and suggestions in her p may perhaps be accommodated by this suggestion. The practice adopted in herd, when fresh blood is deemed necessary, is to introduce it by way of the female

Figure III shows the line of transmission of a character inherited in a sex lin manner. The sex linked factors are marked by a thick line. Where the contribu is through the dam it is designated by a dotted line, for she may be heterozygou the sex linked character, and therefore the contribution in a population should ave at rather over half of that marked by the thick line through the sire.

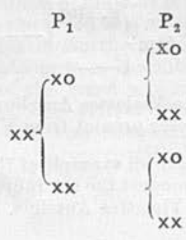
FIGURE III.

Inheritance of a Sex Linked Factor in Cattle.



Alternatively the line of sex linked inheritance might perhaps be better unders by the following diagram.

FIGURE IV.



Since a bull contributes no x chromosome to his sons, all contribution of a sex linked factor to the sons' progeny must be traced through their dams. Therefore the paternal grandparent contributes no sex linked character to his granddaughters.

It will be noticed that half of the sire's pedigree makes no contribution, however good it may be. This is the side that is frequently most emphasised. Altogether, in the fourth parental generation only half the ancestors need be considered in the examination of a pedigree from this point of view. While, in a way, the sire's contribution to the heifer is the more important, it is only so because it is the more definite. The dam has a greater accumulation of blood lines to draw upon, and if there are several sex linked factors involved, may certainly make the bigger contribution on the average.

On making a close study of the work of Gowen and others at Maine in search of facts which might disprove this hypothesis the writer was unable to find anything definite in this direction. On the contrary Gowen, in his book (1924) dealing with American Holstein Friesians from the Advanced Registry, gives figures showing the correlations between daughter and parents and between daughter and grandparents. Table II tabulates his results, and is drawn chiefly from pages 155, 188, 224, 252, 300, 309, 319 and 327.

TABLE II.

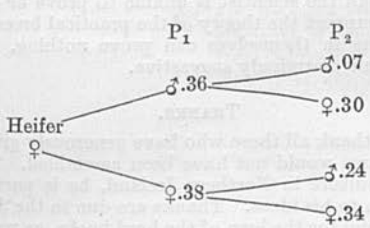
SHOWING CORRELATION COEFFICIENTS OF HEIFERS WITH THEIR PARENTS AND GRANDPARENTS (FROM GOWEN).

		Yield.	P.E.	Butter Fat %.	P.E.
Half	Same sire . . .	·362	±·015	·374	±·015
Sisters	Same dam . . .	·381	±·033	·221	±·036
Daughter to:					
Paternal Grandsire . . .		·070	±·014	·176	±·014
Paternal Grand-dam . .		·297	±·014	·336	±·014
Maternal Grandsire . .		·244	±·016	·224	±·016
Maternal Grand-dam . .		·344	±·021	·258	±·022

Thus, while the parents contribute about equally, there is considerable variation in the grandparents, that of the parental grandsire being considerably and significantly less than the other grandparents. That the correlations are small does not greatly matter. The difference exists, and, as far as the writer is aware, Gowen has made no attempt to explain it. This table may be represented diagrammatically in Figure V.

FIGURE V.

Showing correlation of milk yields with parents and grandparents from Table II.



This squares fairly well with Figures III and IV, showing how sex linked characters are inherited and how the paternal grandsire has no influence in the matter.

Table III shows the correlation figures for cousins by the same grandparents grouped according to the specific grandparent. This forms a useful confirmation of the previous table. The effect of the paternal grandsire in this case is less than the probable error, and may therefore be considered to be nil. The figures for this table are also taken from Gowen's work. For interest the correlations of full sisters and dam to daughter are also added.

TABLE III.

FURTHER CORRELATION COEFFICIENTS OF RELATED COWS.

	Milk Yield.	Butter Fat %.
Cousins by Common:		
Paternal Grandsire	$\cdot005\pm\cdot029$	$\cdot119\pm\cdot029$
Paternal Grand-dam	$\cdot171\pm\cdot045$	$\cdot214\pm\cdot044$
Maternal Grandsire	$\cdot206\pm\cdot020$	$\cdot216\pm\cdot020$
Maternal Grand-dam	$\cdot234\pm\cdot044$	$\cdot244\pm\cdot044$
Full Sisters	$\cdot548\pm\cdot027$	$\cdot464\pm\cdot032$
Mother to Daughter	$\cdot497\pm\cdot021$	$\cdot413\pm\cdot023$

Further, Pearl, Gowen and Miner (1919) in their work on the American Jer give a list of sires in order of their sons' performances as parents of productive hei While certain bulls came out of this study to their credit, there are what the aut call 'certain disappointments.' The greatest of these are the sons of Hood F Torono 60326, who, without exception, lowered the production of their daught Hood Farm Torono clearly led amongst the list of sires in increasing the milk produc of his progeny over that of their dam. There are also other such 'disappointme The sons of imported bulls make a rather better showing, but here again there similar cases, the male progeny of Noble of Oakland being one of them.

Gowen (1925), working with the Guernsey breed, shows how great is the vari in the yields between the sire's daughters and his son's daughters. He states, 'T we could expect from any given grade of sire, whether his daughters were hi low, sons which would have daughters ranging from the highest to the lowest prod in the breed.' Again 'The variation of the sons' daughters in production is practically the same as that of the whole breed.' The point to be gathered from work is that, while the sons tend to revert to the average of the breed, this is nearly so marked in the daughters. Thus further evidence is obtained in favo the hypothesis that one or more of the factors governing milk production, both and butter fat percentage, are inherited in a sex linked manner.

* * * *

This is partly hypothesis, and while the premises on which it is based are exceedi suggestive they cannot yet be taken as absolutely sound. No valid grounds h been found upon which to disprove it, but the matter requires further investiga because, if the hypothesis should bear fruit, it ought to modify the practice of bree to a considerable extent.

The reason for its inclusion in this discussion is because the writer is of op that the ideas and principles that activate enlightened breeders are always worth consideration, even though the scientist is unable to prove or disprove them. in this case facts which support the theory of the practical breeder have undoubte been obtained. Statistics in themselves can prove nothing, but placed along tangible facts they become alarmingly suggestive.

THANKS.

The writer wishes to thank all those who have generously given that help wit which the facts and figures would not have been assembled. To Mr. J. S. Gor of the Ministry of Agriculture in Northern Ireland, he is particularly indebted the study owes its origin to his ideas. Thanks are due to the Jersey Cattle Soci of both Jersey and England for the loan of the herd books, as well as for help in o directions, to the Ministry of Agriculture for the gift of the 'Registry,' and als Mr. Bruce Ward for particulars about his herd. To Dr. H. Corner the write grateful for his suggestions and for his patience and forbearance throughout a len correspondence.

And finally the writer gladly acknowledges the work of Mr. J. R. Brown, B (Agr.), of the Nigerian Agricultural Service, who did all the statistical work, anal the pedigrees and calculated the coefficients. The writer regrets that Mr. Brown unable to conclude this investigation himself.

Summary.

1. In English Jersey cattle cows giving over 1,000 gallons in one lactation are found to be less inbred than the average of the breed.

2. A possible reason for this is that yield is not inherited in an entirely autosomal manner, but that one or more factors governing its production as regards both quantity and quality may be sex linked.

3. Examination of the pedigrees of the high-yielders supported this view as well as the experiences of certain practical breeders.

4. If this were the case, then the paternal grandsire would have little effect on the yield of his granddaughters.

5. Figures are quoted from the work of Gowen which show that the contribution of the paternal grandsire is significantly less than that of the other three parents.

References.

Gowen, J. W., and Mildred R. Covell (1921-1) Studies in Milk Secretion IX. *Maine Agr. Expt. Stat.* Bull. 300.

(1921-2) Studies in Milk Secretion XII. *Maine Agr. Expt. Stat.* Bull. 301.

Gowen, John W. . . (1924) Milk Secretion, Baltimore. Williams & Wilkins Company. Price 20*s*.

Gowen, John W. . . (1925) Studies in Milk Secretion. XVI. Progeny Performance of Guernsey Sires' Sons. *Maine Agr. Expt. Stat.* Bull. 327.

McPhee, Hugh C., and Sewall Wright (1925) Mendelian Analysis of the Pure Breeds of Livestock. III. The Shorthorn. *Jour. Hered.* v. 16, pp. 205-215.

(1926) Mendelian Analysis of the Pure Breeds of Livestock. IV. The British Dairy Shorthorn. *Jour. Hered.* v. 17, pp. 396-401.

Pearl, R., Gowen, J. W., and Miner, J. R. (1919) Studies in Milk Secretion. VII. Transmitting Qualities of Jersey Sires for Milk Yield, Butter Fat Percentage and Butter Fat. *Maine Agr. Expt. Stat.* Bull. 281.

Robertson, E. . . (1921) Notes on Breeding for Increase of Milk in Cattle. *Jour. Genet.* v. xi., pp. 79–90.

Wright, Sewall . .. (1922) Coefficients of Inbreeding and Relationship. *Amer. Nat.* v. 56, pp. 330-339.

(1923) Mendelian Analysis of the Pure Breeds of Livestock. I. The Measurement of Inbreeding Relationship. *Jour. Hered.* v. 14, pp. 339-348.

Wright, Sewall, and Hugh C. McPhee (1925) An Approximate Method of Calculating Coefficients of Inbreeding and Relationship from Livestock Pedigrees. *Jour. Agr. Res.* v. 31, pp. 377-383.

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THE INHERITANCE OF MILK YIELD IN AYRSHIRE COWS

BY

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THE INHERITANCE OF MILK YIELD IN AYRSHIRE COWS

By A. D. BUCHANAN SMITH, M.A., M.S.A., B.Sc. Agr.,
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The possibility that some of the factors governing the inheritance of milk might be inherited in a sex-linked manner has been suggested by one of the writers (1). The need was felt for further investigation. There are two main avenues by which this question may be explored: by planned experiment with cattle or by a study of the existing milk records. The former method is slow and very costly, but would probably give conclusive results. The latter does not require experiment to provide the necessary facts, but the data may be somewhat vitiated by lack of control over conditions of nutrition and husbandry which undoubtedly affect, to a great extent, the amount of milk which a cow may yield in a lactation.

The statistical method uses the existing herd books and milk records, and approaches the question by studying the effect of various animals in the ancestry upon the yields of their female descendants. A sex-linked character cannot be transmitted from a paternal grandsire to his granddaughter. The sex-linked qualities of a bull are all transferred to his daughters while, if a cow is heterozygous for them, only half her offspring will possess them.

Attention must be drawn to the fact that it is not reasonable to expect that all the factors influencing milk yield may be inherited in a sex-linked manner. Milk yield must be dependent on many factors, not merely on those directly connected with secretion of milk, but also on those which govern constitution, size, weight, etc. The purpose of the present paper is to explore the subject further from the statistical aspect in order to find out whether any of the factors governing milk yield are inherited in a sex-linked manner and, if so, how they compare with the factors inherited in the ordinary autosomal manner.

The material was taken from the annual records of the Scottish Milk Records Association and from the Ayrshire Cattle Herd Book. Thirty leading herds of pedigree Ayrshire cattle, all located in the south-west of Scotland and which have been continuously recorded from 1922 to 1928, were selected from their alphabetical order. One other herd, out of alphabetical order, was included, as it had a great effect on many of the other herds.

In all, some 5000 records were obtained, and these eventually represented 1518 cows. The records were corrected for age on the figures of Kay and M'Candlish (2) for Ayrshire cows in the south-west of Scotland. No correction

[1] Now of the Seed Testing Station, Dept. of Agriculture for Scotland.
[2] Now at the Hannah Dairy Research Institute.

was made for the length of lactation, but where the period was under 245 days or over 365 days the record was not taken. Where possible, the results of several lactations were taken, and the average of the corrected yields was considered as the yield for the individual.

At this point it should be emphasised that published milk records are not the ideal material. Owing to the fact that the records of low yielders are excluded from publication, the averages of the low-producing cows whose records are on the border line may be unduly high. In addition, the records of certain low-producing relatives may not be published.

The method for a statistical study is difficult. Direct correlations can be obtained between female relatives, but it is not possible to measure the phenotype of a bull as regards milk yields, and hence a method of indirect correlation must be used. It is thus unfair to compare the indirect correlations to male ancestors with the direct correlations to female ancestors.

In the present study direct correlations have been made where possible. Where this was not possible, indirect correlations have been employed. The mode of indirect correlations used here differs considerably from that employed by Gowen (3), who describes his method (p. 299): "The basis of this method is...the fact that the grandsire must of necessity fall in only one array of the correlation table, since, if we had an actual milk record on this sire, this record could fall in only one column of the table. With this fact and the known relations of the standard deviation of the arrays to the standard deviation of the whole table it is possible to calculate the correlation coefficient."

Since, in actual practice, Gowen found this value to be slightly higher than the product moment value, he used certain correction factors which he described. The method employed in the present paper is similar in principle, but "degrees of freedom" are used in place of correction factors. The writers are greatly indebted to Dr R. A. Fisher for advice and assistance in this part of the work, which otherwise they feel they could not have tackled. The following is an example of the method of indirect correlation between cows and their paternal grandsires.

The yields of 1518 cows were shown to 269 paternal grandsires. Sixty-three of these 269 bulls had six or more granddaughters recorded, making a total of 1121 cows. The mean and standard deviation of the whole table were calculated and the groups from the 63 bulls were withdrawn, and the mean and value Σfd^2 were obtained for each group. (Where the group contained 10 cows or under the value for Σfd^2 was obtained arithmetically, otherwise all calculations were by the short-cut method.) The Σfd^2 values and the $\bar{d}^2$ values were summed, as was the total number of cows in the 63 groups giving:

$$s^2 = \frac{\int\Sigma fd^2}{N - N_1}. \qquad \int\Sigma fd^2 = 8197{\cdot}93. \qquad \Sigma\,\bar{d}^2 = 6{\cdot}00. \qquad \bar{d}^2 = \frac{\Sigma\,\bar{d}^2}{N - N_1}.$$

$N = 1121$ (total number of cows in groups).

$N_1 = 63$ (number of groups).

Class interval = 50 gallons.

Then, taking one degree of freedom from each group, the standard deviation was calculated:

$$\sigma^2 = s^2 - \bar{d}^2 - \text{Shepherd's coefficient}.$$

$$= s^2 - \frac{\Sigma\, \bar{d}^2}{N - N_1} - \text{s.c.}$$

$$= s^2 - \cdot 0057 - \text{s.c.}$$

$$\sigma = \sqrt{s^2 - \frac{\Sigma\, \bar{d}^2}{N - N_1} - \text{s.c. in class interval}}$$

$$= \sqrt{s^2 - \cdot 0057 - \cdot 0833}.$$

$$= 138{\cdot}4 \text{ gallons}.$$

$$\sigma = \text{standard deviation of whole table}$$

$$= 143{\cdot}3 \text{ gallons}.$$

$$\sigma \text{ array} = \sigma \text{ table} \sqrt{1 - r^2},$$

$$138{\cdot}4 = 143{\cdot}3 \sqrt{1 - r^2},$$

$$r = \cdot 259.$$

Table I gives the results obtained in this study by direct and indirect correlations. For convenience the results obtained by Gowen (3) with American

Table I.

Results of this study		Results of Gowen	
Sire and daughter Mainly half sisters but a few whole sisters were included	0·451 ±0·0138	Sire and daughter Only half sisters	0·52 ± ? or 0·58*
		Half sisters to half sisters By the same sire	0·362 ±0·015
Dam and daughter With a few exceptions only one daughter was correlated to each dam. Only an occasional case of full sisters being correlated to one dam	0·418 ±0·038	Dam and daughter "A number of the dams have two or more daughters and thus appear in the dam column twice"	0·497 ±0·021
		Half sisters to half sisters By the same dam	0·381 ±0·033
Granddaughter and paternal grandsire Indirect correlation as described	0·259 ±0·0163	Granddaughter and paternal grandsire Based on correction factor method	0·07 ±0·014
Granddaughter and maternal grandsire Indirect correlation as described	0·478 ±0·0134	Granddaughter and maternal grandsire Based on correction factor method	0·244 ±0·016
Granddaughter and paternal granddam Direct correlation	0·049 ±0·061	Granddaughter and paternal granddam Direct correlation Indirect correlation	0·258 ±0·040 0·297 ±0·014
Granddaughter and maternal granddam Direct correlation	0·131 ±0·053	Granddaughter and maternal granddam Direct correlation Indirect correlation	0·307 ±0·047 0·344 ±0·021
Danish figures			
Dam and daughter	0·343 ±0·029		
Granddaughter and maternal granddam	0·038 ±0·06		

* This figure 0·58 was obtained on Gowen's data by the methods employed in the present study.

Holstein Advanced Registry cows are tabulated on the right. Some Danish figures, the raw material of which was provided by Prof. James Wilson, are also added; these last are from records of about thirty years ago.

From this table two major points emerge. The first is the correlations of granddaughters to the two kinds of grandsire. The correlations obtained are considerably higher than those found by Gowen. Nevertheless the difference is significant, being in this study 0·238, while the results of Gowen's work make it to be 0·174. This is the principal point at issue in the question of sex-linkage.

The high degree of correlation found in the present study may be partly accounted for by the fact that a different method was used. It might also be accounted for by the fact that the material for the two studies differs considerably. The average milk yields in Gowen's work were around 2000 gallons, while in this study they were only about 900 gallons.

The second point that emerges is the low degree of correlation of the granddaughters to their granddams, maternal and paternal. This may be accounted for by the two facts stated above, but it hardly obviates the almost significant lack of correlation to the paternal granddam. On an entirely sex-linked hypothesis this should be one-half that of the sire; while, on an entirely autosomal hypothesis, the correlation should be one-quarter that of the sire. Since, in the present study the correlation is even less than this, other reasons must be sought to explain this difference.

To the writers the probable reason appears to be the fact that the yields of many of the granddams occurred in the earliest years of milk recording, and this was especially so as regards those granddams for which several records were available. Since the importance of milk recording was not at that time fully appreciated as a basis for selective breeding, the early recorded cows were not selected on a yield basis to the same extent as occurs at the present day. Accordingly the yields of the grandmothers show considerable similarity. Further, subsequent improvement has occurred more largely through the bulls than through the cows. Consequently high correlations to the early cows would not be expected. This reason also applies to the Danish figures.

The same explanation might also in part explain the fact that the correlations to the grandsires are higher here than in Gowen's study. There is a higher selection among dairy bulls than among dairy cows. So long as a cow is not possessed of thoroughly bad qualities, she is likely to retain her place in the herd. It has been shown by Roberts (4) and others that dairy herds replenish one-quarter to one-third of their milking cow stock every year. Since comparatively few bulls are required in proportion to the number of cows, a much higher standard has existed and still exists in their selection. While, therefore, the cows of ten years ago (granddams in the present study) tended to be of the average type, and therefore unlikely to give high correlations, the bulls were genetically of a higher type and, therefore, would give higher correlations.

A further possible reason for the extremely low degree of correlation to the paternal granddam may lie in the fact that, as milk recording increased, less attention was paid to exhibition points and more emphasis placed on the results of the records. A proportion of the granddams might, therefore, have been of the exhibition rather than the utility type, and their yields would therefore not be expected to show a strong correlation to those of their granddaughters. As time goes on these difficulties would eliminate themselves, and there is every reason to believe that later generations would show much higher correlations to their granddams.

The lower degree of correlation to the paternal grandsire than to the maternal grandsire, which is the main point in an enquiry into the possibility of any sex-linked inheritance, stands out fairly clearly. It was, however, considered desirable that further investigation should be made along these lines. It was felt that it ought to be possible to test the point by means of direct correlation, and the following method was adopted:

There are two ways by which a figure could be given to the sire. The one is by giving him the average yield of his dam, the other those of his daughters. The former method was thought to be undesirable and the latter, since it might be considered to give some idea of the genotype, was preferred.

If the inheritance of milk yield was entirely autosomal, both the sons and daughters should transmit the qualities of the sire in about equal degrees. If it were in any way sex-linked then the sons would not transmit the qualities to the same extent as the daughters. Accordingly two correlation tables were made up from the data already described. The first correlated the yields of the sires' daughters with the sires' sons' daughters (paternal granddaughters), while the second correlated the yields of the sires' daughters with sires' daughters' daughters (maternal granddaughters). Thus a direct comparison could be obtained of the effect of certain bulls as paternal grandsires as compared with their effect as maternal grandsires. Table II gives the results.

Table II. *Sires' daughters to granddaughters*

Sires' daughters to sires' sons' daughters	$0{\cdot}253 \pm 0{\cdot}07$
Sires' daughters to sires' daughters' daughters	$0{\cdot}322 \pm 0{\cdot}041$

The numbers obtained for this work were not very large, being 81 in the one case and 215 in the other but, although the probable error of the first figure is somewhat large, the results may be taken as fairly significant. There might be some bias in favour of the second correlation, because a certain number of the daughters would be the mothers (and not merely aunts) of the granddaughters. But this could hardly be accepted as explaining the whole difference.

Dr Fisher has kindly drawn our attention to the fact that this method of assigning a genetic value to an individual on the strength of the performance of his progeny is quite accurate, if (i) all males compared have been mated with the same series of females, and (ii) considerable progenies have been raised for each mating. These conditions can be fulfilled with fishes and poultry, but they cannot even be approached with cattle. Accordingly these last results cannot be considered as conclusive, though they should be interpreted in relation to the other results as subsidiary evidence of some sex-linked effect on milk yield. They do serve to show the difficulties that beset the investigation of the problems of inheritance and the slow rate at which animals of economic importance reproduce themselves.

In this paper it was not the purpose of the writers to review the whole subject, but rather to give an interim account of the investigations in hand. These are being pursued by other methods and are being extended to butterfat. Although any individual result so far obtained may possibly be accounted for by other reasons than sex-linked inheritance, the fact that similar results are arrived at by different methods and with different material tends to confirm the impression that sex-linked factors do play a certain part in the inheritance of milk yield. But further work is required before conclusions may be reached, and the results of this paper should be accepted with reserve.

The writers wish to acknowledge the data received through the kindness of Prof. Wilson, the assistance in the corrections of the yields from Mr M'Candlish of the West of Scotland College of Agriculture, and the invaluable advice, explanation and criticism of Dr R. A. Fisher, F.R.S.

REFERENCES.

(1) Buchanan Smith, A. D. (1928). Inbreeding in Jersey cattle. *Proceedings of the Glasgow Meeting of the British Association*, pp. 649–55.

(2) Kay, R. R. and M'Candlish, A. C. (1929). Factors affecting the yield and quality of milk, the age of the cow. *J. Agric. Sci.* **19**, 342–72.

(3) Gowen, J. W. (1924). *Milk Secretion.* Baltimore: Williams and Wilkins Co. Price 20*s*.

(4) Roberts, E. J. (1929). Wastage in dairy herds. *Welsh J. Agric.* **5**, 67–72.

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The Inheritance of Milk Yield

A Paper delivered at the
International Dairy Congress, Copenhagen, 1931

BY

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THERE is adequate evidence to show that amongst the agents conditioning the amount of milk yielded by a cow, the genetic aspect is of considerable importance. Heredity also affects both the quality and quantity of the individual constituents of milk. Our knowledge, however, is still limited concerning qualities other than the yield of butter fat. Owing to the multitude of other factors which also influence both yield and quality of milk, any scientific analysis of the inheritance of milking capacity is beset with peculiar difficulties.

A priori, neither yield nor quality can be inherited in any simple manner. Many factors must be involved since not only does milk secretion depend upon the proper development of the mammary glands and those organs concerned with reproduction and milk secretion proper, but also upon such features as the total size and weight of the animal as well as the development of other organs such as the lungs, the heart and the digestive tract.

Size, for instance, as shown by Gowen (1), Turner (2), and others, has a considerable influence both on total milk yield as well as on butter fat. Size in itself is inherited in no simple manner but is dependent on many genes. The same probably applies to other characters of genetic origin, which, directly or indirectly, are bound to affect the amount and the composition of the milk that a cow may give.

In spite of this, the key to the situation lies in the various milk glands and those organs of internal secretion which directly affect them. Other factors cannot emphasize what is not there, they can only retard or inhibit the possibilities of secretion which primarily reside in the organs of lactation. It is equally reasonable to suppose that the inheritance of these organs may be dependent either on quite a few genes or on many. There is nothing absurd in either supposition. If they are dependent on relatively few genes, and these act in a simple Mendelian manner without dominance, then the result of a statistical study would be similar to that which would be expected if they were dependent on many genes.

The evidence from first crosses between breeds of different levels of production tends to show slight dominance for increased milk production and slight recessivity for increased butter fat yield. If the organs of lactation are dependent for their expression upon a few genes acting in either a definitely dominant or definitely recessive manner, this would be noticed at once in the first crosses of breeds where the progeny would take after one of the parents. This is not the case: so this possibility (i.e. definite dominance or definite recessivity) may be ruled out.

There remain those modes of inheritance, dependent upon a few genes, which do not conform to classical Mendelism. Chief amongst these are the sex-linked and sex-limited modes. Milk Secretion is, in a sense, sex-limited. The purpose of this paper is to describe work which has been done to enquire whether genes inherited in a sex-linked or sex-limited manner have any considerable effect on milk production.

There are two lines along which such an investigation can proceed. Firstly, by means of controlled experimentation with the appropriate reciprocal crosses. In such an investigation it is difficult to eliminate those factors which influence milk yield but are not of genetic origin. In ordinary practice such factors can never be held as constant as the accuracy of Science demands. To minimize their effect it is essential that fairly large numbers should be employed. This is costly and demands an experiment lasting many years.

The other method is to examine existing records and by using very large numbers counteract the effect of other than hereditary factors. This has been the method employed in the following investigations.

Before describing these it might be as well to draw attention to a point which the writers consider worthy of some consideration and which in fact was one of the reasons leading to the belief that it might be profitable to make the subsequent enquiry.

In the construction of the beef breeds considerable inbreeding occurred. Although at the present time this practice is not used to the same extent as formerly, there is evidence to show that the leading breeders of those beef breeds which originated in the British Isles have, since the foundation days, employed this weapon to no inconsiderable extent and are still employing it. On the other hand, in the dairy breeds of the British Isles no inbreeding has characterised their foundation, and in latter days the method has been seldom employed successfully.

This appears to the writers to be hardly a coincidence. The beef breeds were formed before the dairy breeds, and there is every reason to believe that some of those responsible for the foundation of the dairy breeds were prefectly aware of the methods employed by the beef breeders. Indeed there is some evidence to show that the early breeders of dairy cattle did follow the example of the beef breeders but that the results they obtained in so doing did not justify the employment of this method as a means of fulfilling their object.

Experience has shown that it is reasonable to assume that beef qualities are dependent upon multiple factors and that many of the genes which produce the desired phenotype exhibit dominance or partial dominance. Were this not so, the number of " culls " would be fewer for it would be easier to fix beef qualities in an animal if the genes by which they are transmitted were inherited in a recessive or partially recessive manner. As those who have experience of constructive beef breeding know, the number of inferior animals born constitutes a high percentage. This point also shows that multiple factors must be involved. Further, if the genes for beef production were inherited in a recessive, or even in a truly blending manner, then that heterosis, which is so characteristic of crosses between beef breeds, would not be exhibited. Under these circumstances the logical procedure for the constructive beef breeder is to inbreed, provided there are not too many lethals or other recessively inherited deleterious characteristics.

If milk yield and quality were also dependent upon many factors exhibiting dominance or an absence of it, but not recessivity, then inbreeding would have given as good results. This is not the case although there is not the slightest evidence to show that the proportion of recessive lethals is greater in the dairy than in the beef breeds.

With certain of the dairy breeds inbreeding has been practised by a few breeders. A study of the English Jersey by one of the writers (3) led to the thought that where inbreeding had been successfully employed, it was because the factors had been concentrated in a peculiar manner which might be explained by adopting, as a working hypothesis, the idea that some of those genes which played a not unimportant part in the inheritance of yield and quality of milk were transmitted in a sex-linked manner.

The following is typical of several high producing cows whose pedigrees showed inbreeding:—

Mystole Veronica Vol. 30, p. 88	sire	——	
		g. dam	Violettes Aurelius
			——
	dam	Violettes Aurelius	
		——	

Coefficient of Inbreeding (Wright's) to Violettes Aurelius = 6·25.

Sex-linked character present from Violettes Aurelius.

An equal degree of inbreeding is to be found in the following pedigree which, however, was not typical of those of the high producing inbred Jerseys cows studied.

A. . .	sire	Violettes Aurelius	
		———	
	dam	g. sire	Violettes Aurelius
			———
		———	

Coefficient of Inbreeding (Wright's) to Violettes Aurelius = 6·25.

No sex-linked character present from Violettes Aurelius.

Since this study was published, Corner (4) has written a paper on the subject and has tabulated the pedigrees of a large number of inbred dairy cows, chiefly of the Jersey breed, all of which appear to have been inbred along sex-linked lines.

Gowen (5) has made a list of those bulls of the Guernsey breed which have improved the yields of their daughters over the dams of those daughters. From this and other data he has stated that the sons of bulls which have proved themselves to be "improvers" do themselves leave daughters which are no better and no worse than the average of the breed. This remarkable regression, which tends to be confirmed by work presently being conducted by the writers and others at the University of Edinburgh, can be adequately explained on a sex-linked hypothesis.

Sex Chromosome Distribution

P2	Paternal Grandsire	Paternal Grandam	Maternal Grandsire	Maternal Grandam
	x	xx	x	xx
P1	Sire x		xx Dam	
F1		xx Cow		

To test the possibility of the existence of sex-linked factors, and using existing records as material, it was decided to use the principle employed by Gowen of making correlations to the four grandparents. If the correlation to each of the four grandparents is approximately the same then sex-linked factors, if any are present at all, play an unimportant part. If, on the other hand, they do have effect, then the correlation to the paternal grandsire should be significantly less than to the other grandparents, as the above diagram shows.

Table I. gives the results obtained by Gowen (6) and by Smith, Scott and Fowler (7). Unfortunately, a direct correlation to a male ancestor is impossible. Hence the direct correlation to the female ancestors cannot be compared to those figures obtained for male ancestors.

TABLE I.

Measures of Variation in different Kinship Groups.

	Gowen		Smith et al.
	Milk Yield	Butter Fat Per Cent	Milk Yield
Paternal Grandsire	·005 ± 0·029	·119 ± 0·029	·259 ± ·0163
Paternal Grandam	·171 ± 0·045	·214 ± 0·044	·049 ± ·061
Maternal Grandsire	·206 ± 0·020	·216 ± 0·020	·478 ± ·0134
Maternal Grandam	·234 ± 0·044	·244 ± 0·044	·131 ± ·053

All these results show a significantly smaller correlation to the paternal grandsire than to the maternal grandsire and thus tend to support the hypothesis that sex-linked factors are involved. But this indirect method of correlation is not altogether satisfactory and is open to criticism by the statistician. The effect of non-linear regression, for example, cannot be properly accounted for.

Accordingly, on the advice of Dr R. A. Fisher, F.R.S., of Rothamsted, another method was adopted, the argument for which is briefly as follows. The closer the blood relationship between two individuals the more alike they should be. In the case of dairy cows, for instance, the closer they are related to each other the less difference should there be between their milk yields. If heredity plays any part it should be shown by an analysis of this nature. Similarly, by computing the theoretical chromosome distribution for various relationships, both as regards the autosomes and the sex chromosomes, it is possible to discover the relative importance of the autosomes and the sex chromosomes.

The basis of this method consists in the degree of difference in the yields of pairs of individuals of the same kinship. For example the difference between the yields of two cows possessing the same sire and same dam (full sisters) was taken and squared. This figure was then added to the squared differences of other pairs of full sisters, not necessarily possessing the identical sire and dam as belonged to the first pair. 200 such pairs were obtained; the summation of the squared differences as regards total milk yield was found to be 4,964,468 gallons, giving an average for the class of 24,822.

Excluding pairs which involve a comparison between generations (e.g. dam and daughter) and remembering that only females exhibit

TABLE II.

Possible Relationships of Individuals Possessing One or More Common Parents or Grandparents

(Excluding Inter-Generation Relationships)

	Relationship of Sires				
	Same	Whole Brother (Same Sire Same Dam)	Paternal Half Brother (Common Sire)	Maternal Half Brother (Common Dam)	Unrelated
Same	Whole Sisters	....	....	....	Half Sisters (By Same Dam)
Whole Sister — (Same Sire, Same Dam)	....	Double Cousins	....	....	Cousins
Paternal Half Sister (Common Sire)	....	....	....	....	Half Cousins
Maternal Half Sister (Common Dam)	....	....	....	....	Half Cousins
Unrelated	Half Sisters (By Same Sire)	Cousins	Half Cousins	Half Cousins	Unrelated

the phenomenon of milk yield, there are twenty-four possible degrees of kinship if the pedigree is traced only to the grandparents. These are to be found in Table II. The closer degrees of kinship are to be found on the top left-hand corner, and these gradually decrease till at the bottom right-hand corner are found "unrelated" animals having no parents or grandparents in common. For many of these degrees of kinship there is no simple description, but where such exist they have been written in their appropriate place. This is illustrated in Table II.

The material for this investigation has already been described by one of the writers (7). It is sufficient to state here that the data are drawn from the yields of pedigree Ayrshire cows published by the Scottish Milk Records Association. Hence low yielders are omitted. The records come from thirty herds in the south-west of Scotland. The lactations were corrected for age only, and the figure taken as a lactation yield was the average of the total number of recorded lactations. For the majority of the cows the records of more than one lactation were available.

TABLE III.

Differences in the Butter Fat Yield of Pairs of Cows according to their Relationship Classification

	Relationship of Sires								
	Same		Whole Brother (Same Sire, Same Dam)		Paternal Half Brother (Common Sire)		Maternal Half Brother (Common Dam)		Unrel
Relationship of Dams	(I) N	(II) $\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N
Same	200	4150	...	...	7	5988	...	...	158
Whole Sister ... (Same Sire, Same Dam)	41	3285	...	...	...	...	...	...	29
Paternal Half Sister (Common Sire)	2027	4545	3	4292	29	4812	2	1700	2303
Maternal Half Sister (Common Dam)	69	4028	...	...	1	361	...	...	185
Unrelated	6361	4973	415	4742	6435*	6435*	1166	6036	6660

* These figures are correct. The coincidence is remarkable

(I) N = Total Number of Pairs in each Classification Group

(II) $\frac{\Sigma D^2}{N}$ = Mean of Summation of Squared Differences between the Yields of Pairs of Cows in each Group

Total yield of butter fat in pounds and total yield of milk in gallons were the only qualities for which any considerable body of figures were available. Table III shows the result obtained as regards total yield of butter fat.

Several points in this table demand an explanation. In the first place the blanks are many. Some of the degrees of kinship are exceedingly uncommon but this is unavoidable in a class of animals in which not only is inbreeding extremely rare but where the emphasis for improvement is laid upon the sire. Out of twenty-six thousand pairs of cows, 8698 pairs fall in the group which are related to each other by the same sire while another 6890 are connected with each other by a common paternal grandsire. Added to these are 2305 pairs whose dams are related by having a common sire (i.e. maternal grandsire) and it is seen that out of a total of 26,091 pairs there are 17,893 which trace their connection through a male ancestor as compared to 1858 pairs which trace through a female ancestor. (A small allowance must be made for those animals which fall into both male and female relationships, e.g., full brother and sister.)

Not only are there many blanks in the relationship table but there are even more cases where the number of pairs obtained is insufficient for the present purpose. Since a few individuals all possessing the same ancestor in the same position in the pedigree will give rise to a large number of pairs and since such a condition was not infrequently found, experience with the figures suggested that any data based on less than 1,000 pairs was liable to this bias. For instance the yields of ten cows all bearing the same relationship to each other give 45 pairs while 15 such animals give 105 pairs. Thus the influence of one herd may become unduly great.

Out of the twenty-four relationship groups only six have yielded significant figures. This is much to be regretted since it somewhat vitiates the proof of the method which depends on the consistency of the results.

In the Butter Fat results (Table III) it is found that there is a consistent increase in the average of the squared differences as the degrees of kinship widen, starting with 4,973 for animals with the same sire, and whose dams were unrelated, increasing to 6,036, 6,435 and 6,576 for animals possessing one grandparent in common and ending with 7,950 for animals which are unrelated.

If sex-linkage exists it should be revealed in a comparison of the results obtained from the following classes:—

A Comparison of the Yield of Half-Cousins:—

1. *Cows by the same paternal grandsire.*

$$X \begin{cases} B \begin{cases} \underline{D} \\ E \end{cases} \\ C \begin{cases} F \\ G \end{cases} \end{cases} \qquad Y \begin{cases} H \begin{cases} \underline{D} \\ J \end{cases} \\ I \begin{cases} K \\ L \end{cases} \end{cases}$$

2. *Cows by the same maternal grandsire.*

$$W \begin{cases} M \begin{cases} O \\ P \end{cases} \\ N \begin{cases} \underline{Q} \\ R \end{cases} \end{cases} \qquad Z \begin{cases} S \begin{cases} U \\ V \end{cases} \\ T \begin{cases} \underline{Q} \\ A \end{cases} \end{cases}$$

Since the results are approximately the same:—

1. 6435—common paternal grandsire
2. 6576—common maternal grandsire

and since the matings are reciprocal, it may be assumed that sex-linked genes play no considerable part in the inheritance of the yield of butter fat in Ayrshire cows. This is corroborated by a similar figure (6,036) but based on fewer numbers, where the relationship is due to a common paternal grandam.

Turning now to Table IV which deals with total yield of milk in gallons, the significant groups do not show the same consistent increase. Taking the two reciprocal groups already described the results are:

1. 49,931 — common paternal grandsire.
2. 24,218 — common maternal grandsire.

The figure for cows related by the same sire is 35,698 and that for totally unrelated pairs is 45,579.

Bearing in mind that these reciprocal crosses show the effect of the two grandsires it will be seen that there is 100 per cent. more variability amongst the paternal granddaughters of a bull compared to that amongst his maternal granddaughters.

TABLE IV.

Differences in the Milk Yield of Pairs of Cows according to their Relationship Classification.

	Relationship of Sires									
	Same		Whole Brother (Same Sire, Sam Dam)		Paternal Half Brother (Common Sire)		Maternal Half Brother (Common Dam)		Unrelated	
	(I) N	(II) $\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
Same	200	24,822	...	...	7	34,099	...	...	158	32,837
Whole Sister ... (Same Sire, Same Dam)	41	12,260	...	...	...	...	...	...	29	9699
Paternal Half Sister (Common Sire)	2027	27,821	3	1292	29	12,264	2	9425	2303	24,218
Maternal Half Sister (Common Dam)	69	27,176	....	...	1	15,129	...	...	185	33,191
Unrelated	6361	35,698	415	55,920	6435	49,931	1166	44,128	6660	45,579

(I) N = Total Number of Pairs in each Classification Group

(II) $\frac{\Sigma D^2}{N}$ = Mean of Summation of Squared Differences between the Yields of Pairs of Cows in each Group

There are, however, two points which demand attention, the first being that the figure for daughters connected by a common paternal grandsire (49,931) is greater than that for unrelated pairs (45,579). Since there is no known manner of calculating the probable error of this method it is possible that the difference is within the range of the probable error. If it is not, then the result may in part be explained by the fact that amongst the paternal granddaughter groups the extreme limits of milk yields occurred more frequently than in the random sample which provided the data for the unrelated group. At the same time the lowness of the figure for the group with a common maternal grandsire (24,218) must be noted: this is lower than the group with closer relationship, based on approximately the same numbers, where the pairs have the same sire and the same maternal grandsire (27,821).

The second point relates to the result obtained from the group whose dams are unrelated but whose sires have a common dam, i.e. where the kinship depends upon a common paternal grandam (44,128). This is nearly as large as the unrelated group (45,579). On a theory of sex-linkage the figure for this group should approximate that for the group whose connection lies with the maternal grandsire. That it does not do so in this case may probably be explained by the fact that up till quite recently in the Ayrshire breed the bull was selected not on the performance of his dam so much as on the showyard record of his sire. Actually the figure obtained here tallies very well with that found in the previous paper of Buchanan Smith, Scott & Fowler (7) where the same data was used but treated by the correlation method. By the direct correlation method $r = \cdot049 \pm \cdot061$ while in this study $r^* = \cdot032$. Thus the two methods—correlation and difference—square fairly well with each other.

It is not the purpose of this paper to discuss these points in detail, but it is only right that attention should be drawn to them. These apparent anomalies do admit of a genetical interpretation which the consistency of the figures in Table III. might justify. But the authors prefer to adopt a somewhat more cautious attitude until further figures are available.

Furthermore, future studies should not be based, as all previous ones of this nature have been, on the records of best cows: poor yielders must also be included. Should such studies fail to confirm the results already obtained the possibility will arise that the sex-linked factors can only act in the presence of certain autosomal genes which are to be found in the genetic constitution of high-yielding cows. Should this be the case, the importance of the sex-linked factors

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* r is obtained from the following formula :—

$$r = 1 - \frac{\text{figure for group considered}}{\text{figure for unrelated group}}$$

will be considerable as such factors will give, as it were, the final impetus to high milk production. This appears a somewhat more reasonable assumption than that the majority of the genes governing the mammary apparatus should be inherited in a sex-linked manner.

The conclusion, therefore, at which the authors arrive is perhaps not very definite. In view of the scarcity of certain relationship groups and in view of the two points mentioned above, and despite the strong evidence found in the consistency of the figures for butter fat yield, it is considered best that the question should remain open pending further data.

The point to be emphasized here is that it is not unreasonable to assume that a few of the factors affecting the inheritance of milk yield may be inherited in a sex-linked manner: that various pieces of evidence from different sources point to this being the case: and that no evidence has been obtained which tends to disprove this hypothesis.

The authors also wish to draw attention to the novel manner of analysing the inheritance of qualities which Dr R. A. Fisher has suggested to them. Over two years experience of this method has led to the conclusion that its fundamental simplicity, despite the much greater labour involved, makes this system infinitely preferable to those previously used by the writers and other workers in Edinburgh and America. This method can be applied to many problems of biometry. The authors wish to record their very great indebtedness to Dr Fisher for his unceasingly sympathetic assistance and advice. In addition they wish to acknowledge the assistance freely given by many of their colleagues and by students in the Institute of Animal Genetics in the tabulation of the data, for without such help the results could not have been obtained so quickly. To the Director of the Department, Professor F. A. E. Crew, they owe much, not only in opportunity and facilities for the work, but also for his kindly understanding of the difficulties involved.

ABSTRACT.

The paper opens with a general discussion of the inheritance of milk yield and the difficulties in its analysis. The thesis is then put forward that some of the factors governing total yield of milk are inherited in a sex-linked manner. Previous work in support of this hypothesis is quoted.

A new method of investigation suggested by Dr R. A. Fisher is outlined. This method is dependent upon the difference between the squares of the corrected yields of two or more cows related to a common parent or grandparent, that ancestor appearing in the same place in the pedigree of each cow. Unfortunately, the data used did not supply sufficient figures to cover the twenty-four possible relationship groups. In the results concerning the inheritance of butter fat it was found that there is a constant increase in the averages of the squared differences as the degrees of kinship widen. The squared differences are approximately the same in the two groups, firstly where the pairs are half cousins by the same paternal grandsire, and secondly where they are half cousins by the same maternal grandsire.

As regards the inheritance of milk yield there is a significant difference between the differences of the squared yields of pairs of cows related respectively to the common paternal grandsire and to the common maternal grandsire. Since the latter is half the former, it is considered possible that sex-linked factors may be involved.

The conclusion at which the authors arrive is not absolutely definite. The point to be emphasised is that it is not unreasonable to assume that a few of the factors affecting the inheritance of milk yield may be transmitted in a sex-linked manner and that no evidence has been obtained which tends to disprove this hypothesis.

BIBLIOGRAPHY.

1. Gowen, J. W. 1924. Milk Secretion. Ch. III. Baltimore: Williams and Wilkins.
2. Turner, C. W. 1930. The Inheritance of Body Weight in Relation to Milk Secretion. Miss. Agr. Expt. Sta. Res. Bull. 147. Pp. 1–42.
3. Smith, A. D. Buchanan. 1928. Inbreeding in Jersey Cattle. The Possibility of Yield and Quality of Milk being inherited in a Sex Linked Manner. British Association Reprints (N.S.) No. 22. Pp. 649–655.
4. Corner, H. 1930. Line-Breeding for Sex Linked Characters. J. South Eastern Jersey Club. Vol. VI., No. 1. Pp. 10–18.
5. Gowen, J. W. 1925. Studies in Milk Secretion XVI. Progeny Perfomance of Guernsey Sires' Sons. Maine Agr. Expt. Sta. Bull. 327. Pp. 197–252.
6. Gowen, J. W. 1924. Milk Secretion. Ch. XXIII. P. 329. Baltimore: Williams and Wilkins.
7. Smith, A. D. Buchanan, Scott, R. J., and Fowler, A. B. 1930. The Inheritance of Milk Yield in Ayrshire Cows. J. Dairy Research, Vol. 1, No 2, 1930. Pp. 174–179.

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Errata Slip.

Page 20, Table V.:-

The bottom row of figures should read as follows:-

4414 58,665 802 27,822 1442 21,553 1784 91,400

In the same table, the figure at the top of the right-hand column, in place of 62,392, should read 66,553.

For Degree of D. Sc.

STUDIES ON THE INHERITANCE OF YIELD AND QUALITY OF MILK IN DAIRY CATTLE.

By

A. D. Buchanan Smith, M.A., B.Sc.(Agr.), M.S.A.

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Presented to the Faculty of Science of the University of Edinburgh for the Degree of Doctor of Science.

Introductory Note.

Since 1928 the writer has been investigating the possibility that sex-linked genes affect the inheritance of milking capacity in cattle. The thesis presented herewith describes a final study on this subject from the angle of existing records of herds managed commercially. It is supported by a series of papers dealing with this subject. The size of the statistical data required help in its collection and analysis. For the conclusions drawn therefrom, and for the general discussions contained therein the writer is entirely responsible, the work of the co-authors being confined to collection and tabulation of the data. The principal paper is being submitted for publication, the secondary is being published in the Scientific Proceedings of the International Dairy Congress held recently in Berlin.

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CONTENTS.

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A STATISTICAL ENQUIRY INTO THE INHERITANCE OF MILK YIELD IN THREE HERDS OF DAIRY SHORTHORN CATTLE.

By

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PART ONE.

The Enquiry and its Results.

Under the best of circumstances it is seldom easy to trace the mode of the inheritance of a quantitative character. When the expression of that character is also conditioned by environmental factors, the difficulties increase. A slow reproductive rate further retards the enquiry, but perhaps the crowning tribulation is when the expression of the character is restricted to one sex. Such are the troubles that afflict an investigation into the inheritance of milk yield in cattle. And they are further magnified when it is remembered that milking capacity is not a unit character, but comprises many facets which are themselves both quantitative and qualitative.

Yet the fact that the mode of inheritance may be a complicated one is no argument against the importance of the genetic basis in the manifestation of that character. That, in pre-mendelian days, we understood nothing concerning Heredity did not diminish the part it played. It is, however, occasionally argued that if a character is transmitted in a complicated manner then, even supposing we obtain a full knowledge of the mode of its transmission, it will not be possible to use that knowledge to practical advantage. There is some truth in such an argument, but there are plenty of instances to the contrary.

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In fact it is neither possible, nor reasonable, for us to say that knowledge, at present hidden, will, when discovered, be of no practical use. In the history of Science there are many examples where an apparently useless piece of knowledge has been discovered to be the essential clue to the solution of some practical problem.

This argument is not infrequently used when an attempt is made to apply the principles of Genetics to the productive qualities of slow breeding animals which must, _a priori_, be dependent upon a multitude of genes, the cumulative effect of which gives the appearance of a kind of blending inheritance. But if sex-linked genes - or even autosomal genes which act in an inhibitory manner - in any way condition the expression of the character, then, if they are of major importance, it is essential that allowance be made for them, for they must affect the practical considerations involved.

It is easy to select for a character inherited as a simple recessive. As regards other kinds of autosomal inheritance (dominance, incomplete dominance, or multiple factor), improvement can be fairly easily effected by the intelligent use of the Progeny Test. But with sex-linked genes the Progeny Test, while it may allow for a certain measure of improvement, is but a/

a slight improvement upon the existing method of mass selection.

The principal obstacles which beset a study of the inheritance of milk yield have never really been appreciated. In the first place milk yield, which is itself a quantitative characteristic, must be dependent for its expression upon a number of genes. Multiple factors must be involved since genes which do not affect the organs of milk secretion may still have greater or less effect upon the yield. It may be argued that a few factors primarily affecting the organs of milk secretion are mainly responsible. However, as expression of such genes as increase milk yield may be inhibited by other genes which influence other parts of the body of the cow, the general effect is bound to be one of multiple factors. Nevertheless it may be possible, with suitable material, to discover the mode of transmission of a few of these major factors.

The second obstacle is the effect of environment upon yield, and the difficulty of getting figures in which the differences can be fairly interpreted as being primarily of genetic origin. Of all the obstacles this has been the one which has been most clearly recognised. Many studies, such as those of Gowen (1), have been made with exceedingly large numbers/

numbers in the hope that, by this means, environmental effect would be evened out. Von Patow (2) has made a noble effort to overcome this by means of his "byre-average" whereby all the yields recorded in any one year are corrected by a comparison with the yields in other years. There is, however, a grave danger lest the adoption of such a correction factor flattens out the genetic influences which are at work.

The third difficulty is that the yield of milk is limited to one sex only. Therefore correlations with male relatives are impossible. Yet if a study of variation is to be made, such a comparison is indispensible, both from a scientific and a practical point of view. Unless the influence of the different parents and grandparents can be measured on a comparable basis, it is not possible to arrive, by means of the statistical method, at any conclusion whatsoever concerning the mode of the inheritance of milk yield: nor is any practical information available as to the relative importance of different ancestors in the pedigree of any animal. To meet this difficulty methods of "indirect correlation" have been used first by Gowen (1) and then by Gifford and Turner (3), Buchanan Smith (4) and others. But these proved unsatisfactory for various reasons, particularly that the indirect correlations to male relatives could not be compared to the direct correlations to female relatives./

relatives.

To overcome this difficulty another method, devised by Dr. R. A. Fisher, has been already employed by the present writer (5). Briefly the argument is as follows: the closer the blood relationship of two animals, the more genes they should have in common, the more alike they should be, and, in the case of dairy cattle, the less difference there should be between their milk yields. The difference between the yields of any two cows may be measured by subtracting the lower from the higher yield and squaring the difference. Thus the difference between cows, according as they are differently related, may be compared. The unit of calculation is a pair of cows similarly related.

In the first study by this method there were 200 pairs of full sisters, that is to say each cow of a pair had the same sire and the same dam. There was, of course, a diversity of sires and dams, but the link binding each pair of cows was the fact that they both possessed the same sire and the same dam. The squared differences for each pair were then added together and divided by the number of pairs, and this figure, $\frac{\Sigma D^2}{N}$, was taken as the index of variability which occurred in the yields of animals thus related. The squared difference ~~basis of comparison~~ of a random sample of pairs of unrelated cows was taken as a basis of comparison since this could be assumed/

assumed to be 100% variability within the group studied. The figures previously obtained (5) are shown in Table I.

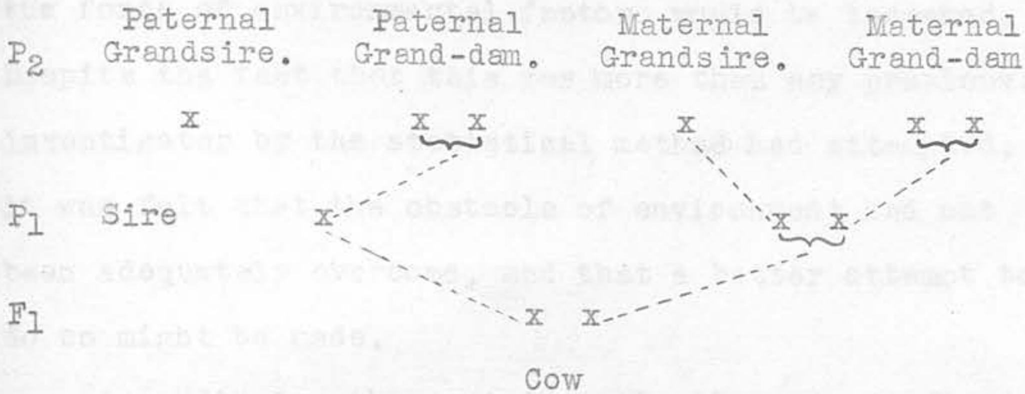
TABLE I

Differences in Milk Yield and Butterfat Yield of Pairs of Ayrshire Cows according to their Relationship Classification.

	Number of Pairs.	Milk Yield.	Butter Fat Yield.
	N	$\frac{\Sigma D^2}{N}$	
(1) Full Sisters.	200	24,822	4,150
Half Sisters:			
(2) by same sire with dams also half sisters.	2,027	27,821	4,545
(3) by same sire with dams unrelated.	6,361	35,698	4,973
(4) by same dam with sires unrelated.	158	32,837	4,358
Cousins:			
(5) by sires which are full brothers with dams unrelated.	415	55,920	4,742
Half-Cousins:			
(6) Same paternal grandsire.	6,435	49,931	6,435
(7) Same maternal grandsire.	2,303	24,218	6,576
(8) Same paternal grand-dam.	1,166	44,128	6,036
(9) Same maternal grand-dam.	185	33,191	5,389
Unrelated Pairs:			
(10) Random Sample.	6,660	45,579	7,950

An/

An examination of this table shows that as the degrees of kinship widen, the figures representing the variability in milk yields also increase, with one or two exceptions. The figures for butterfat yield show a remarkably steady increase. The basal figure for comparison is that of the unrelated pairs (Class 10) and, as regards total yield of milk, this is 45,579. Two of the figures for the related groups (Classes 5 and 6) exceed this and these are the figures for paternal full cousins and for half-cousins whose only near ancestor in common is the paternal grandsire. The figure for paternal full cousins is based on small numbers, and is perhaps somewhat biassed, due to the fact that a large number of pairs in this group traced to the same full brothers. The other group which shows extreme variation is the group whose only near ancestor in common is the paternal grandsire. This fact, together with the fact that the figure (Class 7) for half-cousins tracing to the same maternal grand:
:sire is lower than was anticipated, has been explained by us as possibly being due to the fact that some of the factors governing the inheritance of milk yield are transmitted in a sex-linked manner. If this were the case, then the influence of the paternal grandsire is much diminished as the following diagram shows :-



The fact that the method employed is sound may be seen from the similar figures obtained for yield of butter:fat which are placed in the third column, and which show a fairly consistent increase in variation as the degrees of kinship widen, culminating in the highest figure for pairs of unrelated cows.

The data on which these figures were based suffered from certain defects, which indeed were common to all previous studies by the correlation method. In the first place the data consisted of the published records of cows. Since low records are omitted from publication, it was considered possible that this might account, in some undefinable manner, for the fact that the maternal grandsire appeared to exert a greater influence on his grand-daughters than did the paternal grandsire.

By confining this study of Ayrshire cows to thirty herds in the same part of Scotland, and all managed under similar conditions, it was hoped that the/

the force of environmental factors would be lessened. Despite the fact that this was more than any previous investigator by the statistical method had attempted, it was felt that the obstacle of environment had not been adequately overcome, and that a better attempt to do so might be made.

Accordingly, the next investigation was confined to three large herds of Dairy Shorthorns, and each herd was treated as a unit, only lumping them together for the final analysis. Thus the records of each cow in a pair were made under practically identical circumstances. Where more than four years elapsed between the record of one cow and that of the other of the pair, the records were discarded.

The index of yield for each cow was calculated by correcting the actual yield for age according to the figures Sanders (6) obtained for Dairy Shorthorns, and then taking the average of the number of age-corrected lactations available. In no case was the record of a cow based on less than two lactations. Any lactation extending over a greater period than 365 days or less than 245 days was discarded, as also were those where the interval between calvings exceeded fifteen months. Since the figures were taken from the private records of the breeders, and not from published sources, it was considered that it included all/

all grades of yielders and thus eliminated a possible source of error which had existed in all previous studies. Unfortunately adequate figures for butterfat were not available. The results are shown in Table II.

TABLE II.

Difference in Milk Yield of Pairs of Dairy Shorthorn Cows from Three Herds According to their Relationship Classification.

(Each herd treated separately but the results lumped together.)

	Number of Pairs. N.	$\frac{\Sigma D^2}{N}$
(1) Full Sisters.	191	38,644
Half Sisters:		
(2) by same sire with dams also by same sire.	2,506	32,822
(3) by same sire with dams unrelated.	11,903	44,155
(4) by same dam with sires unrelated.	215	59,577
Cousins:		
(5) by sires which are full brothers.	248	33,329
Half Cousins:		
(6) by same paternal grandsire.	3,627	62,856
(7) By same maternal grandsire.	8,737	47,499
(8) by same paternal grand-dam.	1,021	45,318
(9) by same maternal grand-dam.	667	47,684
Unrelated Pairs:		
(10) Random Sample.	7,573	78,357

Here/

Here again, with the exception of the group of half cousins by the same paternal grandsire (Class 6), the figures, where large enough, show a consistent increase as the degree of kinship widens. That the kinship group where the relationship of the pairs is based on the paternal grandsire again shows this aberration implies that this cannot be due to chance, particularly as it confirms the results obtained by less reliable methods and data. We are thus inevitably forced to the conclusion that there is some complicating factor which operates in the transmission of milk yield from one generation of cattle to another. This point is more fully discussed in a subsequent portion of this paper where the results are examined in detail.

It was suggested to us by Dr. Fisher that the results obtained might be translated into correlation figures by the use of the following formula:

$$r = 1 - \frac{\text{figure for group considered}}{\text{figure for unrelated cows}}$$

Accordingly we give, in Table III, the correlations thereby obtained in order to give an estimate ofthe degree of similarity existing among cows of the same group.

Caution is required in the interpretation of these figures. The figure for unrelated cows is not the best that might be used. To express the true genetic variance the figures for unrelated cows should be/

be based not, as has been done, on pairs of cows contained in the same data, but rather on pairs of cows of as many breeds and crosses as possible, but maintained under identical environmental conditions. There is no doubt that if it were possible to secure such data it would give a bigger variance. Accordingly the correlation figure r which we have given must in every case be too small. This is, however, only of importance when it comes to a consideration of the relative forces of Heredity and Environment. r does not interpret the full genetic influence of the common ancestor involved, but it does provide a guide within the breed (or herd) to the relationship between an ancestor and its descendant.

TABLE III/

TABLE III.

Correlations in respect of Herd A only.

	r =	Number of Pairs.
(1) Full Sisters.	+ .679	123
Half Sisters:		
(2) by same sire with dams by same sire.	+ .539	2,020
(3) by same sire dams unrelated.	+ .323	9,543
(4) by same dam sires unrelated.	+ .364	100
Cousins:		
(5) by sires which are full brothers.	+ .432	248
Half Cousins:		
(6) by same paternal grandsire.	+ .035	2,083
(7) by same maternal grandsire.	+ .351	6,883
(8) by same paternal grand-dam.	+ .380	273
(9) by same maternal grand-dam.	+ .338	476

PART TWO.

Detailed Examination of the Results.

In view of the fact that the method employed in this investigation is a new one it deserves some examination, particularly since it is suitable for the analysis of other genetic problems which involve quantitative inheritance and especially so when the expression of that quantitative character is limited to one sex though transmitted by both.

In Appendix ~~III~~ will be found tables giving in I
detail the results obtained, firstly in respect of the Ayrshire cattle examined in the previous study, secondly in respect of each of the three herds on which this study is based, and thirdly as regards the largest of these three herds in respect of two separate sections, the low yielding and the high yielding animals.

The first point of interest is the number of blanks in the relationship tables. Some of the degrees of kinship are exceedingly uncommon, but this is unavoidable in a class of animals in which not only is inbreeding rare, but where the emphasis for improvement is laid upon the sire. As already pointed out, in the Ayrshire data out of 26,091 pairs of cows, 17,893 traced their connection through a male ancestor as compared to 1,858 pairs whose connection depended on a female ancestor. In the present study 36,116 pairs were involved/

involved, and of these 2,172 were connected by a female ancestor whereas 27,463 traced through a common male ancestor. (Allowance must be made for animals which fall into both male and female relation: :ships.) Such a difference is only to be expected in a breeding population where the females outnumber the males by somewhere about 25 to 1.

There are some interesting differences in the numbers falling into the different kinship groups in respect of the two studies. For instance there is a considerable increase in the proportion of the pairs of Dairy Shorthorn cows which are by the same sire as compared to the Ayrshire data. The number of cows on which each study is based are approximately the same, being 1518 in the case of the Ayrshires, and 1536 in the present examination. Similar increases are found where the sires are unrelated and the dams are half-sisters, either paternal or maternal. These cannot be considered to be breed differences between the Dairy Shorthorn and the Ayrshire. The Dairy Shorthorn data is confined to three large herds, and consequently a greater increase would be expected in the proportion of pairs by a common sire or a related dam as compared to the Ayrshire data where there were thirty herds, and all comparatively small.

This explanation appears to be borne out by the fact/

fact that the Dairy Shorthorn data shows a decrease in the number of pairs where the sires are whole brothers, and this decrease is reproduced by a marked decrease in the number of pairs where the sires are paternal half-brothers. Apparently the tendency amongst these Dairy Shorthorn breeders has been to avoid using in their own herd sires which are either full-brothers or which possess a common sire. Is this tendency indicative of a subconscious recognition of the fact that the influence of the paternal grandsire is of lesser importance than that of the other parents ?

With the example of the creators of the Beef Shorthorn before them, the Dairy Shorthorn breeders have shown more inclination for inbreeding than the Ayrshire men. This is exemplified by an increase in the proportion of the pairs whose sires and whose dams have both a common sire, i.e., the group where the sires are paternal half-brothers and the dams paternal half-sisters.

Turning now to an examination of the figures of each of the three herds that constitute the present study, an analysis of the data for each of the three herds in respect of the relative influence of each of the grandsires is interesting. The crucial figures are as follows :-

TABLE IV./

TABLE IV.

Kinship Group.	Herd A.		Herd B.		Herd C.	
	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
(5) Sires Paternal half brothers. Dams unrelated.	2,083	56,629	1,435	66,553	109	133,175
(6) Sires Unrelated. Dams Paternal half sisters.	6,883	38,086	1,368	71,845	486	101,850
(9) Unrelated Pairs.	4,414	58,665	1,784	91,400	537	201,593

Thus it will be seen that only two of these herds, A and C, show an increased variation due to the paternal grandsire, while Herd B shows a slight tendency in the opposite direction. The difference is great in respect of Herds A and C and may be taken as significant since in Herd A it amounts to some 30% of the total variation of the unrelated pairs, and in Herd C to 15% of the total variation. In Herd B, however, it is less than 6% of the total variation.

This anomaly in respect of Herd B may be interpreted in one of three ways. First it may be interpreted as implying that the paternal grandsire is of equal importance with the maternal. The results of the Ayrshire data and of the other two herds would then have to be explained as due to chance. This is rather too far-reaching an assumption to make, and, if it is maintained, it can equally be said - and with three times as much likelihood of being correct - that the figure in respect of Herd B is due to chance, while the three others are the correct ones.

But, granting that the difference between Herd B and the other results are significant, then it may be argued that if there is an important sex-linked gene acting, and a lot of genetic variance besides, it is possible that Herd B is homozygous, or nearly so, for the sex-linked gene. This is a not unreasonable assumption./

assumption.

A third interpretation may be obtained from a more detailed analysis of the figures. In this investigation, after the figures for Herd A had been analysed, and before starting on the records for Herd B, it was deemed advisable to investigate the method so far as selected groups of cows were concerned. Herd A was accordingly divided into two groups of high and low yielding cows respectively according as they gave over or under 700 gallons. These groups were then treated as separate units. The detailed results are to be found with the others in the appendix. There is reason to believe that they furnish the reason for the figures obtained in respect of Herd B. The salient facts are as follows :-

TABLE V./

TABLE V.

Degree of Kinship	HERD A.						HERD B.	
	Entire Herd		High Yielders		Low Yielders		Entire Herd	
	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
(5) Sire Paternal half brothers. Dams unrelated.	2,083	56,629	392	16,774	1,171	17,237	1,435	62,392
(6) Sires unrelated. Dams paternal half sisters.	6,883	38,086	1,087	16,652	3,087	17,303	1,368	71,845
(9) Unrelated.	5,252	61,327	1,853	30,027	1,983	24,879	1,784	91,400

A study of the whole of Herd A has revealed the fact that, where the common ancestor of each pair of cows was the paternal grandsire, the variance approximated the variance found in the whole herd, and was nearly 50% greater than where the pairs of cows traced to a common maternal grandsire. But when these cows were divided into two groups of high yielders and low yielders this difference was not apparent. In each of the two divisions of the herd the variance of the two classes of half cousins is, in this respect, the same. This may be interpreted as indicating that the sex-linked factor acts as a major modifying gene in that it always appreciably modifies the yields of the cows by depressing or increasing them to a considerable extent.

Thus the reason why no difference was obtained in respect of these two groups of half cousins in Herd B may be easily explained, especially since an examinat: :ion of the data showed that the owner of Herd B had been discarding from his herd before the completion of their second lactation a far larger proportion of cows than had the owners of Herds A or C. Correspondence with the owner of Herd B confirmed this deduction. It is thus fairly clear that in Herd B we are dealing with a group of cows already selected for their high yields, and that this fact has obscured the true action of/

of a possible sex-linked gene.

These figures may be looked at also from another angle. The average lactation yield of all the cows of Herd A is 642 gallons. The dividing line was off the centre at 700 gallons. There were 388 High yielders with an average of 824 gallons, and there were 567 Low yielders with an average of 575 gallons.

If the herd were divided equally, then in the group of unrelated cows the individual cows should be found equally on both sides of the dividing line. This being the case, a high yielding cow should have an equal chance of being compared either with another high yielding cow or with a low yielding cow. If the low yielders are excluded, the high yielding cow can only be compared with another high yielding cow, and the number of pairs possible for comparison is reduced by a half. If 50% of all the cows are high yielders, theoretically the possible number of pairs of high yielders is only 25% of the total number of pairs of unrelated cows in the whole herd. Similarly, as regards low yielders, the possible number of pairs is only 25% of the total number of pairs of unrelated cows in the whole herd.

Then, (without allowing for the fact that the herd has not been quite equally divided) in respect of the/

the unrelated pairs, the total number of pairs of each of the two sub-divisions of the herd should be approximately half the total number of pairs for the whole herd. This is the case, the total number of pairs of the two sub-divisions amounting to 51% of the whole. That is to say 49% of the pairs of the whole herd have been lost by the sub-divisions: such pairs are referred to as <u>divided pairs</u>.

Genetic factors increase the similarity in yield between related pairs, therefore, in the case of related pairs, the chance increases that a high yielder will more likely be paired with a high yielder and that low yielders will stand a better chance of pairing with low yielders. Accordingly, the number of <u>divided pairs</u> should be less than 50%. This appears to be the case, though not remarkably so, except in one instance. Where the numbers are considered signific: :ant the percentage of <u>divided pairs</u> in respect of each relationship group is as follows:-

<u>TABLE VI</u>./

TABLE VI.

Herd A. Division of Pairs of High and Low Yielders.

	No. of Pairs in whole herd.	Percentage divided pairs.
(2) Sires, same dams, paternal half Sisters.	2,020	48%
(3) Sires same. Dams unrelated.	9,543	45%
(6) Half cousins. Same paternal grandsire.	2,083	25%
(7) Half cousins. Same maternal grandsire.	6,883	40%
(9) Unrelated Pairs.	4,414	49%

The significant point here is the fact that where half cousins are related by a common paternal grandsire 75% of the pairs fall into one or other of the two groups. (This figure is perhaps unduly high owing to the fact that the herd has not been equally divided, but that this is not a big objection is seen from the comparatively even distribution of the other groups.) But, within each sub-division of group 6 the variab:ility is the same as that to be expected if the inheritance were autosomal (Table V). The variability found for this group in the whole herd is not the sum of the variabilities found in respect of 75% of the total number of pairs which fall into the high and low yielding/

yielding sub-divisions, (i.e., 56,629 is not the sum of 16,774 + 17,237). Their variabilities combined are roughly the same as the variability of the group of half cousins tracing to a common maternal grandsire (38,086). The fact that in the whole herd the variability of half cousins tracing to a common paternal grandsire is so much greater implies that the cause for great variability must lie in the 25% of divided pairs.

Hence this variability must be of a very high order indeed. The individuals which comprise the divided pairs instead of each having yields lying, the one just below 700 gallons and the other just above that figure, (as must be the case in the other relationship groups), must have yields extremely far apart, and in all probability beyond the average of each of the sub-divisions. The average lactation yield of the High yielding cows is 824 gallons, while that of the Low yielding cows is 575, the difference being 249 gallons. If, in the entire herd, the variability of this group of half cousins tracing to a common paternal grandsire is due to a sex-linked factor, and if this sex-linked factor is not expressed in respect of 75% of the pairs examined, it follows that the extreme variability of the 25% is an indication of the variability due to the sex-linked gene/

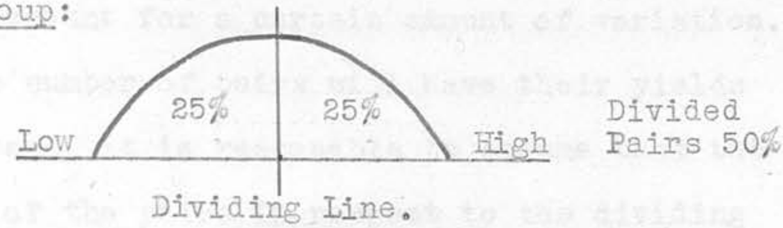
gene which consequently appears to have an effect of some 250 gallons in a herd of cows whose average yield is 650 gallons. In other words, it may be postulated that there is a sex-linked gene which conditions the total yield of milk, and which, in this case, affects about one-third of the total yield. The reason why this "scatter" is not seen in the random sample of the unrelated pairs is that the unrelated pairs, when sub-divided, do not have the autosomal inheritance to link the pairs together, and consequently to reduce the percentage of divided pairs.

As regards the other relationship groups, all of which approach 50% of divided pairs, the fact that the index of variation is not as different (although, of course, there is a big difference) as in the case of the relationship group tracing to a common paternal grandsire, indicates that the yields of the divided pairs of the other relationship groups are closer to each other and nearer to the average. This may be expressed diagrammatically as follows:-

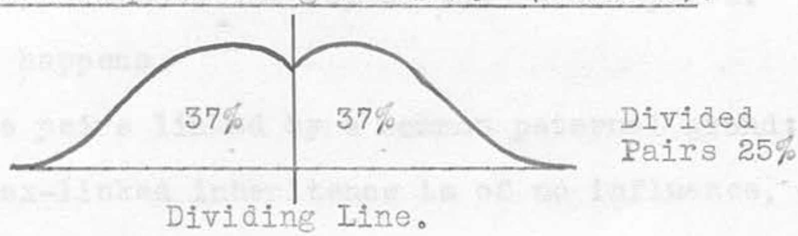
<u>FIGURE I</u>./

FIGURE I.

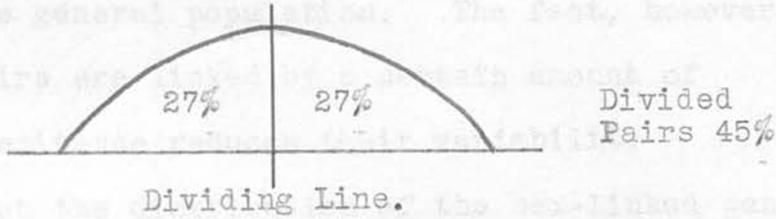
Unrelated Group:



Related by common paternal grandsire. (Class 5):



Other relationship groups:



In effect, the argument is this: If only a sex-linked factor operates a random population should be divided into two classes. But if autosomal factors also operate (as they most certainly do in this case), the sex-linked factor will not segregate the population into two distinct classes. The autosomal factors have already given rise to great variation which the sex-linked factor will only accentuate without dividing the population. The related groups other than that possessing a common paternal grandsire will show a reduced variation in the yields of the pairs owing to the fact that both the autosomal and the sex-linked/

linked inheritance reduce this variation. Environment is bound to account for a certain amount of variation. Since a large number of pairs will have their yields near the average, it is reasonable to assume that the distribution of the pairs in respect to the dividing line should approximate the 50% of the random pairs. This is what happens.

With the pairs linked by a common paternal grand:sire, the sex-linked inheritance is of no influence, and sex-linked genes operate more or less at random as they do in the general population. The fact, however, that these pairs are linked by a certain amount of autosomal inheritance reduces their variability somewhat. But the distribution of the sex-linked gene roughly divides this group of pairs into two classes, with the result that only 25% of all the pairs in this group are separated by the dividing line.

In view of the fact that in this relationship group the 25% of divided pairs must show a very high degree of variability, it is reasonable to assume that, for this 25%, the yields of each individual must fall, in the case of the low yielders, near or below the average of the low yielders, and, in the case of the high yielders, near or above the average of the high yielders. The difference in the averages of the low and high yielders is approximately 250 gallons, and this may be taken as about the difference in the yields of/

of the divided pairs. As it has been argued that the differences in the divided pairs are primarily due to the random effect of the sex-linked gene, it is then possible to make the deduction that the effect of the sex-linked gene is of the order of 250 gallons in a population of cows averaging about 650 gallons.

The next step is to determine the manner of the inheritance of the sex-linked gene, dominant, recessive, or intermediate. Were it recessive it might be assumed that the population could soon become homozygous for it. But the fixing of a recessive that is both sex-linked and sex-limited is not so easy as the fixing of a simple recessive. Nor can it be said that breeders have intensively selected for such a recessive, for they have other characters for which they must select their stock, and the effect of sex-linkage may be masked by autosomal inheritance.

In another paper (7) dealing with the variance in the progeny of different bulls whose daughters are out of the same population of cows and were in-milk at the same time, it has been shown that such bulls may have their daughters with very different degrees of variance, although the average yield of the daughters of the bulls is approximately the same. The paper referred to was based on the data of the three herds used in the present study. This fact points to a certain degree of/

of dominance either in the autosomal or the sex-linked genes, or both.

In order further to examine this point the variance of the progeny of the different bulls was examined in relation to the average yield of the progeny. Only when a bull had at least six daughters meeting these conditions were his progeny considered. As only 9 such bulls were found in Herd C this was eliminated from the calculations. The results for the other two herds are as follows :-

TABLE VII..

Variance in the yields of daughters of different bulls correlated with the average yield of the daughters.

	r	P.E.	N	Average Yield of Herd.
Herd A	+ 0.33	± .09	43	660 gallons
Herd B	+ 0.43	± .11	24	858 "

These figures are not conclusive but indicate that, as the yield increases, so does the variance of the daughters. If this is so it is an argument against dominance in any high degree.

In order to clear up the point that the Standard Deviation, measured in gallons, may not be comparable at all yields, it was decided to test the coefficient of variation in correlation with the average yields. For the data in Herd A it was found that r = - 0.17 ± .08. This/

This means little, and does not confirm the previous result. This method is probably an over-correction.

Another test could be made by ascertaining if the regression of the Standard Deviation on yield was higher among tested bulls than it is between different herds. Accordingly the following calculations were made :-

TABLE VIII./

TABLE VIII.

Showing coefficients of correlation and regression among daughters of selected bulls as compared to the cows in the two divisions of Herd A.

Data.	Coefficient of Correlation. (S.D. and Yield)	Coefficient of Regression. (S.D. on Yield)	Average Yield. (gallons)
Herd A selected.	+ 0.33 ± .09	$x_1 = + .2080\ x_2$	660
Herd B selected.	+ 0.42 ± .08	$x_1 = + .2467\ x_2$	858
Herd A high yielders.	+ 0.89 ± .03	$x_1 = + .9215\ x_2$	787
Herd A low yielders.	- 0.42 ± .08	$x_1 = - .3540\ x_2$	570

These figures tend to confirm the previous deduction that the genetic factors affecting high yield do not act in an exclusively dominant manner.

The data obtained in this study may be analysed still further. In so far as they throw light on the "Progeny Test" of dairy bulls, the results are to be found in a paper dealing with this subject exclusively (7). The figures could also be used as a measure for inter-herd (and with the Ayrshire data) for inter-breed variation from which might be deduced certain information concerning environmental effects: the various figures in the different relationship groups may be employed as a measure for the comparative influence of male as against female ancestors: a preliminary examination in these directions was made, but it soon became evident that to arrive at a definite conclusion would be straining the data some:what, and that further studies of this nature would be required for statistical accuracy. Accordingly, the detailed figures are given in Appendix I, so that anyone embarking on a similar enquiry may, by comparison with these figures, be enabled to draw further conclusions concerning the inheritance of this fascinating, but extremely complex, problem which is of fundamental importance to what is possibly the most important product of Agriculture.

PART III.

Review and Conclusions.

In 1928 the present writer put forward the suggestion that the inheritance of total yield of milk might be in part conditioned by the action of sex-linked genes. This was founded on a study by the writer of the Jersey breed in England (9) and an examination of the results obtained by Gowen (1) for the Holstein breed in America. In Gowen's work it was found that the correlation to the paternal grandsire was considerably less than that to the maternal grandsire. This finding has since been confirmed by the work of Buchanan Smith, Scott and Fowler (4) with the Ayrshire breed in Scotland, and by Madsen (8) with the Red Danish breed. In the present study the figures of Herd A were analysed by this method with the following results, which confirm the previous work :-

TABLE IX.

Correlations to Paternal and Maternal Grandsires.

Correlation.	
Sires' daughters to Sires' Sons' daughters.	r = - 0.20 ± .16
Sires' daughters to Sires' Daughters' daughters.	r = + 0.43 ± .13

These methods were based on indirect correlation and/

and so were not altogether satisfactory. Accordingly, on the advice of Dr. R. A. Fisher, the method of the squared difference employed in the present work was used in an examination of data from 30 herds of Ayrshire cows. As regards butterfat yield (in lbs.) no difference was found between pairs of cows according as to whether they traced to a common paternal or maternal grandsire: but as regards milk yield the difference was substantial. This difference, as regards milk yield, is confirmed in the present work.

The original observation of the possible existence of a sex-linked factor was made more than nine years ago, and in the interval no direct evidence has been led against this observation despite the fact that several workers are engaged upon the problem. Without leading evidence in support, Gowen (15) reports that sex-linked factors do not operate. Fohrman and Graves (16), working with American Ayrshire cows, report finding no evidence of sex-linkage, but their enquiry was not so directed to enable them to determine this point. Copeland (17), who has obtained figures in harmony with the sex-linked hypothesis, is inclined to attribute the differences to environment and methods of selection. Leroy (18), in a brief review of the subject, states that neither fat nor milk yield is sex-linked. Taufer (19) is of opinion that sex-linkage may exist, and quotes the work of Bogdanor to this effect/

effect in the case of the inheritance of fat.

The original criticism concerning the method of the correlations has been met, and subsequent results, by the improved method, have confirmed the earlier deductions.

Another criticism was in the fact that it was unjust to compare yields of cows of one generation with those of another. These have also been met by the present method which only compares the yields of cows milking almost simultaneously with each other.

A third criticism which was valid in respect of all the earlier work, including the study of Buchanan Smith and Robison (5) by the squared difference method, was that the grand-daughters of paternal grandsires were more likely to be distributed throughout different herds than the grand-daughters of maternal grandsires, and therefore their yields would be more subject to environmental influences. This last criticism has been met in the present paper by confining the yields compared to cows in one herd only.

Thus all the major objections have been met and there is still evidence of the fact that the paternal grandsire has less influence on the yields of his grand-daughters than has the maternal grandsire. And no evidence in the contrary direction has been obtained./

obtained.

The practical implications of this result are that, in the selection of a bull for a herd, undue emphasis should not be placed on his sire. It is to the good that he should be a proven good sire since he is then bound to have some of the desired autosomal genes. But as regards the desired sex-linked gene, this can only be obtained by the bull from his dam, and therefore the yield of the dam of a bull is of prime importance. As long ago as 1925 Gowen (10) showed that the sons of proven good sires do themselves leave daughters which are, on the average, no better and no worse than the average of the breed. This has since been confirmed by other studies.

The other implication refers to inbreeding. If sex-linkage is important, then for inbreeding to be effective it cannot work by the concentration of the blood of a famous sire through his sons. In this connection it is interesting, and perhaps significant, to note that inbreeding has not been employed successfully as a means for the creation or improve:
:ment of the dairy breeds, although it has been of the greatest use to the breeders of beef cattle. This is particularly marked in the case of the Shorthorn breed, where the Dairy Shorthorn men have had every temptation to employ inbreeding but have not done so. One is almost drawn to the deduction that some Dairy Shorthorn/

Shorthorn breeders must have tried inbreeding, but without success. Furthermore, examinations which have been made of the coefficients of inbreeding of high yielding dai ry cows as compared to the average of the breed usually show the high yielders to be less inbred. Fowler (11) has shown this for the Ayrshire, and Buchanan Smith for the English Jersey (9) and for the Shorthorn (unpublished).

In previous papers (12, 13, 14) the present author has reviewed all the literature on the subject of the inheritance of milk yield generally, and has discussed in detail the question of sex-linkage. For the convenience of readers of this paper, previous results, as they bear on the question of sex-linkage, are to be found tabulated in Appendix II.

The conclusion of this paper must be on a personal note. It is the writer's opinion that, for the solution of problems concerning the improvement of our slow-breeding farm animals, the statistical method based on large numbers of animals nurtured under different environments, can never be more than a reconnaissance of the general problem. There can be no question that milking capacity is dependent for its transmission on a large number of genes interacting with each other. Some of these will almost certainly be borne on the sex chromosomes. The point is whether these sex-linked genes are of major importance.

To/

To this it cannot be said that the present studies have given a conclusive answer. The most that has been accomplished so far is an indication that sex-linked genes may have a certain effect, and that there is certainly no substantial evidence pointing in the other direction. Even if it should be later shown that a sex-linked gene does not operate, the curious aberration of the figures of yields of cows related by a common paternal grandsire will have to be explained. The one thing that can be definitely concluded from these studies is that there is something peculiar. If this peculiar thing is not genetic, but environmental, it requires to be discovered, since it most certainly influences the standard of selection by which the breeder of dairy cattle operates. The problem, therefore, calls for a solution if the yields of dairy cattle are to be improved.

Until the physiologist links up with the geneticist so that the immediate and not the ultimate action of the different genes that affect milking capacity can be determined, it is unlikely that any definite information will be obtained as to the mode of inheritance of specific genes. Present investigations can only lead us to an uncertain determination that a certain gene affects, say, total yield of milk. We really want to know <u>how</u> that gene affects/

affects the yield of milk, e.g., through a full-functioning of the pituitary gland. Then it will be possible to discriminate one gene from another and to trace the mode of its inheritance.

In the meantime the proof of the pudding is in the eating of it and the information we require now is whether sex-linked genes do or do not play a major part in the transmission of milk yield in order that we may modify our method of selection accordingly. For myself, I feel that the only way by which there is a hope of getting this information is by a planned experiment in a herd where environmental effect has been reduced to a minimum. I am convinced that further statistical study of the type cited in this paper cannot give conclusive results which will be sufficient for practical work. We must know whether sex-linkage is of practical importance in this problem. Accordingly I do not propose to make any further investigations of this nature for the magnitude of the task of analysing such data is not commensurate with the degree of accuracy of the results obtained.

SUMMARY.

The paper is an examination of the possibility of sex-linked genes affecting the transmission of milk yield. To reduce environmental effect the study was restricted to three herds of the English Dairy Shorthorn breed, and each herd was considered as a unit. Fisher's Squared Difference method was used.

The lumped results confirm previous work to the effect that the Paternal Grandsire has a lesser effect than the Maternal Grandsire. In this respect the figures for one herd did not agree with the other two.

The largest herd (which showed this difference) was divided into two sections, high and low yielders. These sections did not show any difference in the relative effect of the two grandsires. The implications of this are discussed, and it is tentatively suggested that if sex-linkage operates it has a considerable effect of some 250 gallons on an average yield of 600 gallons.

The whole subject is reviewed, and the author concludes that the accuracy of the conclusions which may be drawn from statistical studies of this type are not commensurate with the labour involved. As a primary reconnaissance such studies have definite value, but planned experimentation is now required in order to resolve the problem.

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BIBLIOGRAPHY.

(1) GOWEN, J.W. (1924). Milk Secretion. Williams and Wilkins, Baltimore.

(2) PATOW, C. v. (1930). Weitere Studien über die Vererbung der Milchleistung beim Rinde. Ztschr. Zücht. B., 17: 3-159.

(3) GIFFORD, W. and TURNER, C.W. (1928). The Mode of Inheritance of Yearly Butter-Fat Production. An Analysis of the Progeny Performance of Ayrshire Sires and Dams. Missouri Agric. Expt. Sta. Res. Bull. 120, 1-52.

(4) SMITH, A. D. Buchanan, SCOTT, R. J., and FOWLER, A. B. (1930). The Inheritance of Milk Yield in Ayrshire Cows. J. Dairy Res., 1: 174-179.

(5) SMITH, A. D. Buchanan, and ROBISON, O. J. (1931). The Inheritance of Milk Yield. Intern. Dairy Cong., Paper No. 4: 127-140.

(6) SANDERS, H. G. (1927). Variations in Milk Yields caused by Season of the Year, Service, Age, and Dry Period, and Their Eliminat:ion. Cambridge University Press.

(7) SMITH, A. D. Buchanan, and ROBISON, O. J. (1937). Variations in the Milk Yields of the Daughters of Different Bulls. World's Dairy Congress, 1937.

(8) MADSEN, K. (1932). Inheritance of Milking Capacity. Nature, 129: 165-166.

(9) SMITH, A. D. Buchanan. (1928). Inbreeding in Jersey Cattle. Brit. Assoc. Rpt., 22: 649-655.

(10) GOWEN, J. W. (1925). Studies in Milk Secretion XVI. Progeny Performance of Guernsey Sires' Sons. Maine Agric. Expt. Sta. Bull. 327: 197-252.

(11) FOWLER, A. B. (1932). The Ayrshire Breed of Cattle: A Genetic Study. J. Dairy Res., 4: 11-27.

(12) SMITH, A. D. Buchanan, and ROBISON, O. J. (1933). The Genetics of Cattle. Bibliographia Genetica, 10: 104 pp.

(13) SMITH, A. D. Buchanan. (1935). Physiology of Dairy Cattle - Genetics. J. Dairy Res., 6: 272-281.

(14) SMITH, A. D. Buchanan. (1937). Physiology of Dairy Cattle - Genetics. J. Dairy Res., 8: 131-142.

(15) GOWEN, J. W. (1934). Influence of Inheritance and Environment on the Milk Production and Butterfat Percentage of Jersey Cattle. J. Agric. Res., 49: 433-465.

(16) FOHRMAN, M. H., and GRAVES, R. R. (1933). Analysis of the Advanced Registry Records of 611 Daughters of 51 Ayrshire Sires. Tech. Bull. U.S. Dept. Agric. No. 349: 60 pp.

(17) COPELAND, L. (1934). Pedigree Analysis as a Basis of Selecting Bull Calves. J. Dairy Sci., 17: 93-102.

(18) LEROY, A. M. (1936). Paper presented at Congress of Animal Breeding, Paris, December, 1936. Abst. Rec. Méd. Vét., 113: 232-239: 1937.

(19) TAUFER, J. (1932). Příspevek k otázce pohlavní limitace dědičnosti dojivosti a mléčného tuku u skotu. Vést. Československ. Akad. Zemedel., 8: 578-581.

Table 10.

Ayrshire Cows - Buchanan Smith and Robison, 1931.

Differences in the Butter Fat Yield of Pairs of Cows according to their Relationship Classification.

RELATIONSHIP OF DAMS.	RELATIONSHIP OF SIRES. Same (I) N	Same (II) $\frac{\Sigma D^2}{N}$	Whole Brother (Same Sire, Same dam) N	Whole Brother (Same Sire, Same dam) $\frac{\Sigma D^2}{N}$	Paternal Half Brother (Common Sire) N	Paternal Half Brother (Common Sire) $\frac{\Sigma D^2}{N}$	Maternal Half Brother (Common Dam) N	Maternal Half Brother (Common Dam) $\frac{\Sigma D^2}{N}$	Unrelated N	Unrelated $\frac{\Sigma D^2}{N}$
Same	200	4150	...	...	7	5988	...	...	158	4358
Whole Sister (Same Sire, Same Dam)	41	3285	...	...	...	...	...	...	29	3270
Paternal Half Sister (Common Sire)	2027	4545	3	4292	29	4812	2	1700	2303	6576
Maternal Half Sister (Common Dam)	69	4028	...	...	1	361	...	...	185	5389
Unrelated ...	6361	4973	415	4742	6435+	6435+	1166	6036	6660	7950

+ These figures are correct. The coincidence is remarkable.

$(I)_N$ = Total Number of Pairs in each Classification Group.

$(II)\frac{\Sigma D^2}{N}$ = Mean of Summation of Squared Differences between the Yields of Pairs of Cows in each Group.

Ayrshire Cows - Buchanan Smith and Robison, 1931.

Differences in the Milk Yield of Pairs of Cows according to their Relationship Classification.

		RELATIONSHIP OF SIRES.									
		Same		Whole Brother (Same Sire, Same Dam)		Paternal Half Brother (Common Sire)		Maternal Half Brother (Common Dam)		Unrelated.	
		N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
RELATIONSHIP OF DAMS.	Same	200	24,822	...	...	7	34,099	...	...	158	32,837
	Whole Sister (Same Sire, Same Dam)	41	12,260	...	...	...	...	...	...	29	9699
	Paternal Half Sister (Common Sire)	2027	27,821	3	1292	29	12,264	2	9425	2303	24,218
	Maternal Half Sister (Common Dam)	69	27,176	...	...	1	15,129	...	...	185	33,191
	Unrelated ...	6361	35,698	415	55,920	6435	49,931	1166	44,128	6660	45,579

Total Number of Pairs of Cows. = 26,091.

Average Lactation Yield in Gallons. = 910. S.D. = 159.5.

Number of Cows. = 1,518.

TABLE 12.

Summary of Data on Dairy Shorthorns - Milk Yield.

Herd.	No. of Cows.	No. of Pairs.	Average Lactation Yield.	S.D.	S.E.
Herd A Complete	955	26,315	642	145.0	± 3.38
" High Yielding	388	4,106	824	103.5	± 2.55
" Low Yielding	567	10,756	575	87.5	± 2.58
Herd B	369	7,523	830	196.0	± 7.21
Herd C	212	2,278	721	238.0	±11.7
Combined Herds	1536	36,116	698	134.5	± 2.44

Dairy Shorthorns - Combined Herds.

Differences in Milk Yield of Pairs of Cows according to their Relationship Classification.

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother.	
	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$
Same	191	38,644	6	27,225	21	69,351	...	...	215	59,577
Whole Sister	15	78,584	...	...	...	...	...	...	13	37,761
Paternal Half Sister	2506	32,882	11	50,769	177	41,521	5	19,506	8737	47,499
Maternal Half Sister	16	29,731	...	...	2	165,698	...	...	667	47,684
Unrelated	11903	44,155	248	33,329	3627	62,856	1021	45,318	6735+	78,732

Total Number of Pairs of Cows = 36,116.

Average Lactation Yield. = 698. S.D. = 134.5.

Number of Cows. = 1,536.

+ Another random sample for this group gave 7573 pairs and $\frac{\sum D^2}{N}$ 78,357.

TABLE 14.

Dairy Shorthorns - HERD A.

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother.	
	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$
Same	123	18,827	6	27,255	1	14,884	...	...	100	37,337
Whole Sister	9	50,926	...	...	...	...	...	...	...	...
Paternal Half Sister	2020	27,057	4	31,919	118	32,769	...	...	6883	38,086
Maternal Half Sister	12	20,840	...	...	2	165,698	...	...	476	38,864
Not Sister	9543	39,705	248	33,329	2083	56,629	273	36,348	4414	58,665

Total Number of Pairs of Cows = 26,315.

Average Lactation Yield. = 642 galls. S.D. = 145.

Number of Cows. = 955.

TABLE 15.

Dairy Shorthorns - HERD B.

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother.	
	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$	N	$\frac{\sum D^2}{N}$
Same	34	39,667	...	...	20	72,081	...	...	104	82,616
Whole Sister	2	25,065	...	...	...	...	...	...	13	37,761
Paternal Half Sister	204	51,986	7	61,526	59	59,023	5	61,526	1368	71,845
Maternal Half Sister	4	56,402	...	...	...	...	...	...	168	79,550
Not Sister	1568	53,007	...	...	1435	66,553	748	48,592	1784	91,400

Total Number of Pairs of Cows = 7523.

Average lactation yield. = 830. S.D. 196.0

Total Number of Cows. = 369.

TABLE 16.

Dairy Shorthorns - HERD C.

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother	
	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
Same	34	109,311	...	...	...	...	...	...	11	43,932
Whole Sister	4	167,578	...	...	...	...	...	...	...	...
Paternal Half Sister	282	68,794	...	...	...	...	...	...	486	101,850
Maternal Half Sister	...	...	...	...	...	...	...	...	23	38,848
Not Sister	792	80,254	...	...	109	133,175	...	...	537	201,593

Total Number of Pairs of Cows = 2278.

Average Lactation Yield. = 721. S.D. 238.0

Number of Cows. = 212.

TABLE 17.

Dairy Shorthorns - HERD A - High Yielding Cows.
(700 galls. and over)

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother.	
	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
Same	31	12,211	...	...	1	13,225	...	...	45	16,156
Whole Sister	...	...	...	...	...	...	...	...	...	...
Paternal Half Sister	293	11,482	8	20,679	14	23,128	...	...	1087	16,652
Maternal Half Sister	6	59,549	...	...	6	8,186	...	...	39	10,527
Not Sister	1354	13,144	28	14,492	392	16,774	...	...	802	27,822

Total Number of Pairs of Cows = 4,106.

Average Lactation Yield. = 824. S.D. 103.5

Total Number of Cows. = 388.

TABLE 18.

Dairy Shorthorns - HERD A - Low Yielding Cows.
(Under 700 galls.)

	Same.		Whole Brother.		Paternal Half Brother.		Maternal Half Brother.		Not Brother.	
	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$	N	$\frac{\Sigma D^2}{N}$
Same	63	12,391	1	14,161	5	16,239	...	...	69	17,008
Whole Sister	6	31,316	...	...	...	...	...	...	8	14,472
Paternal Half Sister	764	14,693	2	42,027	38	29,579	...	...	3087	17,303
Maternal Half Sister	8	30,774	...	...	...	...	...	...	99	16,059
Not Sister	3894	13,748	68	26,105	1171	17,237	31	13,275	1442	21,553

Total Number of Pairs of Cows = 10,756.

Average Lactation Yield. = 575. S.D. 87.5

Total Number of Cows. = 567.

APPENDIX II.

Correlations, etc., showing the relative effect of the Paternal and Maternal grandsires upon the milking capacity of their grand-daughters.

Gowen (1924) — American Holstein.

Grand-Daughter to Paternal Grandsire	- Milk Yield	+ .070 ± .014.	Butterfat %	+ .176 ± .014
" " Maternal "	- " "	+ .244 ± .016	" "	+ .224 ± .016
Half Cousins by Paternal Grandsire	- " "	+ .005 ± .029	" "	+ .119 ± .029
" " " Maternal "	- " "	+ .206 ± .020	" "	+ .216 ± .020

(1934) — American Jersey.

Pairs by common Paternal Grandsire	- Milk Yield	+ .02 (489,526 pairs).
" " " Maternal "	- " "	+ .12 (64,150 pairs).

Buchanan Smith, Scott & Fowler (1930).

Scottish Ayrshire.

Grand-daughter to Paternal Grandsire	Milk Yield	+ .259 ± .016
" " " Maternal "	" "	+ .478 ± .013
Sires' daughters to Sires' sons' daughters .... (i.e. Paternal g.sire link)	" "	+ .253 ± .070
Sires' daughters to Sires' daughters' daughters .... (i.e. Maternal g.sire link)	" "	+ .322 ± .041

Smith & Robison (1931). Scottish Ayrshire.

(Correlation based on Squared Difference method).

Grand-daughters by same Paternal Grandsire	- Milk Yield	- .1	Fat Yield	+ .19
" " " " Maternal "	- " "	+ .469	" "	+ .173

Madsen (1932). Red Danish.

Bulls to Paternal Grandams - Milk Yield + .026 Butterfat Yield + .061

" " Maternal " - " " + .112 " " + .134

Standard error varies from + .03 to ± .04.

Note:

This study is of the genotype of bulls and therefore the crucial correlations are to the grandams, thus showing the relative importance of the sire and dam in the transmission of milking capacity to the bull.

Copeland (1934). American Jersey.

Paternal Grandsires' daughters to Grandsons' daughters - Butterfat yield + .250 ± .036

Maternal Grandsires' daughters to Grandsons' daughters - " + .427 ± .036

Transmitting ability of three Jersey Bulls in lbs. Butterfat.

Grandsire	Daughters		Paternal Grandsons		Maternal Grandsons	
	No.	Average Yield	No.	Average yield of their daughters.	No.	Average yield of their daughters.
Pgg	119	693.88	12	580.86	10	619.04
F.P.	62	728.08	5	557.52	5	604.22
H.F.T.	72	637.34	14	581.03	22	600.57

Copeland attributes the higher average yield of the maternal grand-daughters as due to the fact that there is a tendency for the daughters of maternal grandsires to be a more highly selected group than the sons of paternal grandsires. He notes that the dams of tested sires are highly selected group.

Buchanan Smith (1937). English Dairy Shorthorns.
(This study)

(Correlation based on Squared Difference method)

Grand-daughters by same Paternal Grandsire - Milk Yield + .198

" " " " Maternal " - " " + .394

Herd A only:

Grand-daughters by same Paternal Grandsire - Milk Yield + .035

" " " " Maternal " - " " + .351

By indirect correlation, Herd A:

Sires' daughters to Sires' sons' daughters - Milk Yield - .20 $\pm$ .16
(i.e. Paternal g.sire link)

Sires' daughters to Sires' daughters' daughters - " " + .43 $\pm$ .13
(i.e. Maternal g.sire link)

VARIATIONS IN THE MILK YIELDS OF THE DAUGHTERS OF DIFFERENT BULLS.

By

A. D. Buchanan Smith.

---------oOo--------

Paper read at the International Dairy Congress, Berlin, 22nd - 28th August, 1937.

During recent years a great deal of attention has been devoted to the question of the progeny testing of dairy bulls. The worth of the bulls have been differently estimated, either as the simple average of the yields of all his daughters, or as some expression of their yields in relation to those of their dams. Hitherto little or no attention has been paid to the amount of variability to be found amongst the yields of the daughters of different bulls.

There have been many detailed descriptions of the yields of the daughters of various proven sires. A study of these figures indicates that, whereas a good sire raises greatly the yields of those of his daughters who are out of low-producing dams, yet, when he is mated to high-producing cows, it is rare that any of his daughters exceed their dams. It cannot be denied that there are a certain number of instances where the yields of high-yielding daughters are a substantial increase upon those of their dams. In many of these cases the difficulty has been to distinguish between the effects of environment and heredity. It is probably easier, by adequate methods of nutrition and management, to push up the yields of a potentially high yielder than those of a low yielder. Thus, the difference between a 1,500 and a 2,000 gallon cow may be largely a question of management, whereas the difference between a 600 and a 900 gallon cow may rather be due to the hereditary constitution. In other/

other words, it is probably easier to push a 1,500 gallon cow up to 2,000 gallons than to push a 600 gallon cow up to 900 gallons.

The difficulty of distinguishing the effect of environmental factors as they affect the individual records of the cows has, in some quarters, brought under suspicion the methods adopted for proving a dairy sire. Thus environment may play a big part in the distribution of the yields of the daughters of a bull. In the case of the ordinary testing of a dairy bull the degree of variation amongst the yields of his daughters might be greatly influenced by the variability amongst the yields of the dams of those daughters.

With a view to overcoming these environmental difficulties a study was made of the inheitance of milk yield in three large herds of Dairy Shorthorn cattle in England. Although there was a certain exchange of animals between these three herds, each herd was considered as a separate unit. The method adopted for the study was that suggested by Dr. R. A. Fisher, F.R.S., and already employed by the authors (1) in a study dealing with the inheritance of milk yield in Ayrshire cattle. It consists in the analysis of the degree of difference in the yields of pairs of individuals of the same kinship. The present paper deals with a part of this study, relating only to half-sisters/

sisters sired by the same bull. The method adopted for evaluating the variance amongst the daughters of a bull is based on the difference of the yields of the pairs of daughters of that bull. The difference between each possible pair was squared, and the sum of the squared differences of all the available pairs constituting the daughters of one bull was divided by the number of pairs, thus giving the figure $\frac{\Sigma D^2}{N}$ which can be employed to show the relative variance of the different bulls. In all 76 bulls possessing at least six daughters were analysed in this manner.

As the three herds were under somewhat different systems of management, the amount of variance is seen to be very different. This difference may be environmental or it may be genetic. The present paper does not deal with inter-herd variance, but only with intra-herd variance. Thus the figures for each herd should be considered separately.

Furthermore, the available data was spread over a long period of years, during which changes may have taken place in the management of the herds, and concerning which reliable information is not available. However, since the three herds were large, it was seldom that there were ever less than two sires in use at the same time, and frequently there were more. Accordingly, the results, as well as being divided into herds/

herds, have been further sub-divided into groups. The bulls falling into each of these groups were used more or less simultaneously in the herd, and were used over a period of years. Especially in the cases where there are a large number of daughters it was found that a cow would be served the one year by one bull and the following year by the other bull. Thus, while the populations of cows served by the different bulls in the sub-group are not identical, they are as similar as can be hoped for under conditions other than deliberate experimentation.

The yields of the daughters are age-corrected, using Sanders' correction factor for Dairy Shorthorns. More than 75 per cent. of the yields are based on the average of two or more lactations. All abnormal lactations were discarded. In each case the owners of the herds kept full records of incidence of disease, accident, etc., as affecting the individual lactation yields.

There is not space to tabulate the results of all the 76 bulls thus analysed, but a sample has been made which is illustrative of the whole of the data which has been obtained. In the tables the bulls are identified by consecutive numbers in each herd. Each group of bulls is divided by a line and those falling within each group were in use in that herd over the same period/

period, and their daughters were in-milk at the same time.

HERD A.

Bull Ref. Number.	No. of daughters	Average Yield (Gallons)	Range (Gallons)	$\frac{\Sigma D^2}{N}$
1	32	604	363-1063	51,195
2	9	621	493-832	38,646
3	8	721	642-843	13,183
6	58	675	466-960	21,908
7	35	631	404-839	21,894
8	29	634	464-938	24,354
13	26	661	471-799	17,213
14	17	573	352-749	35,241
15	41	669	369-897	30,232
28	6	799	623-1046	71,144
29	16	573	378-823	35,870
31	29	598	365-1057	49,035
32	36	647	378-908	35,494
33	9	693	606-779	7,448
37	10	700	529-886	26,232
38	41	639	389-883	36,389
39	15	641	302-1175	93,279

As regards Herd A, bulls 1, 2, and 3 were used at the same time: there was little substantial difference between bulls 1 and 2, but No. 3 was distinctly better as regards the average yield of his daughters, the variation of whose yields was considerably less than those of the daughters of the other two bulls: in the case of No. 3 there is an instance of a high average yield and a low variability.

Of/

Of bulls 6, 7, and 8, forming the second group, there was little difference either as regards average yield or variability. Of the bulls in the next group, No. 13, which has a large number of daughters, has low variability: No. 14 was a bad bull as judged by the Progeny Test, and his daughters showed average variability: No. 15 was a better bull, with his daughters showing much the same variability as the poor one. Bull 28 had only six daughters with a high average yield, and very high variability, whereas No. 29, used in the same population of cows, was a poor bull, with daughters of average variability. Bull 33 had few daughters, but of high average yield, and exceptionally low variability compared to those bulls whose daughters were in-milk at the same time. In the last group in this herd bull No. 39, with fifteen daughters, had the greatest variability of all the bulls used in the herd.

HERD B./

HERD B.

Bull Ref. Number	No. of daughters	Average Yield (Gallons)	Range (Gallons)	$\frac{\Sigma D^2}{N}$
6	23	818	500-1338	68,131
7	29	1001	691-1403	68,861
8	9	718	643-838	5,839
9	14	800	472-989	51,178
10	9	847	463-1209	157,932
15	10	830	491-1420	152,417
16	9	893	610-949	18,893
22	12	886	688-1202	45,983
23	6	959	827-1087	25,167

In Herd B, bulls Nos. 6 and 7 both possessed a large number of daughters showing the same degree of variation, but the daughters of bull No. 7 were infinitely better as regards their average yield than those of bull No. 6, although there was only 65 gallons difference between the highest yielding daughters of each bull. Bulls 8, 9, and 10, whose daughters were in-milk at the same time, show an extreme difference in their variability, bull No. 8 being the second lowest in variation in the herd, bull No. 10 being the highest: both 8 and 10 had nine daughters apiece. Bulls 15 and 16 furnish another good example of where there is no great difference between the average yields of the daughters, but there is a tremendous difference in/

in the variability of these yields. Bull 23 shows a high average yield with low variability.

HERD C.

Bull Ref. Number	No. of daughters	Average Yield (Gallons)	Range (Gallons)	$\frac{\Sigma D^2}{N}$
4	24	682	417-1026	60,803
5	18	878	378-1269	67,565
6	7	730	430-960	62,791
7	7	988	556-1539	247,820
8	6	714	469-985	54,331
9	8	666	287-1055	97,787
10	7	708	430-1007	57,336

In Herd C bulls 4, 5, and 6 have daughters with approximately equal variability, but very different average yields. Bull No. 7, with only seven daughters, shows the highest average yield of the bulls in the herd, as well as by far the highest variability.

A careful study of the figures does not disclose any connection between the number of daughters of a bull and the degree of variability. Nor is there any apparent connection between the average yield of the daughters and the variability of their yields.

Looking at the subject from the point of view of the improvement of dairy cattle, it is obvious that what/

what is required is a bull whose daughters have a high average yield with small variation amongst their yields. Apparently this type of bull does exist.

In view of the fact that there also occur bulls which leave some high-yielding daughters and some low-yielding daughters, the deduction might be made that some of the major factors governing the inheritance of milk yield are transmitted in a dominant manner.

It is not the purpose of this paper to discuss such implications, but rather to draw attention to this fact of the variability of daughters' yields, and to the importance of the consideration of this aspect of the Progeny Test if substantial progress is to be achieved by the use of the Proven Sire.

Reference :-

SMITH, A. D. Buchanan and ROBISON, O. J. 1931. The Inheritance of Milk Yield. Internat: :ional Dairy Congress, Copenhagen, 1931. Conference Papers, English Edition, pp.127-140.

Summary :-

This paper deals with the amount of variability in the yields of the daughters of dairy sires. Data from three herds of Dairy Shorthorns shows how extreme this variability may be. Certain bulls exist whose daughters' yields deviate but little from the average, and there are others, the yields of many of whose daughters are far removed from the average.

The implications are briefly discussed.